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THE EFFECTS OF 2,4-DICHLOROPHENOXYACETIC ACID ON MUSTARD PLANTS AS MODIFIED BY LIGHT QUALITY

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BY

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INTRODUCTION

For the past decade the effects of 2,4-dichlorophenoxyacetic acid (2,4-D) on plant growth have been widely investigated. Nevertheless, the overall mechanism by which 2,4-D kills plants is still a problem to plant scientists. It is well-known that 2,4-D may affect plants in many ways. One of the first obvious effects is that of a change in the water relations of tissues. 2,4-D has been observed to cause an initial increase in the moisture content of numerous plants followed by a definite decline until death. The absorption of mineral ions is often depressed by 2,4-D and changes are induced in the amino acid and protein contents. Also, 2,4-D has an effect on the carbohydrate content, photosynthesis, respiration, etc.

The fact that 2,4-D may either promote or retard photosynthesis and/or respiration is well established. However, the exact nature of its initial effects is debatable because numerous investigators have observed that it interferes with many plant mechanisms. Crafts (22) sums up this point as follows:

> Many of the mechanisms being studied may have only a remote relation to the actual method by which the lethal action of a herbicide is brought about. For example, it is tempting to suggest that because the substituted urea and triazine herbicides block photosynthesis, the plants die of starvation. However, if seedlings are placed in complete darkness at the same time that others are treated with these herbicides, the chemically treated seedlings die much before those placed in the dark. And if the concentration of one of these herbicides is sufficient, seedlings of weeds are killed without emerging; in other words,

> they die without ever starting photosynthesis. This emphasizes the point that the actual mode of lethal action is more basic than photosynthesis; the effects on photosynthesis may be secondary to some much more fundamental process that is upset by the herbicide.

Various environmental factors have been studied in relation to their influence on the effects of 2,4-D on plant growth. How different factors may modify the action of 2,4-D remains unclear. Of the many factors studied in relation to the effectiveness of 2,4-D and other herbicides, there is little doubt that light plays a very important role. In a recent monograph Audus (6) points out that the herbicidal action may be effected by a light effect on the absorption process of the plant. This would be an indirect action, accelerating the removal and distribution of auxin from the leaves, thus influencing translocation of food which 2,4-D accompanies, and finally, an activation of 2,4-D in the cell.

Many complications are met when modifying herbicidal action with light. In some instances low intensities have increased the effectiveness of a 2,4-D solution of a specific concentration, whereas the same solution with higher light intensities produced relatively little effect on the plants. In fact, they were almost insensitive to the herbicide. Often, it is important as to whether the plants receive light before or after 2,4-D treatment (6).

This dissertation is a report of a study designed to offer further elucidation of the modifying effects of light qualities on the action of the sodium salt of 2,4-D with the hope of achieving an increased understanding of how

different light colors influence the herbicidal activity of 2,4-D. Tibbitts and Holm (69) emphasized the importance of an understanding of the physiological and morphological responses of plant tissues to phytotoxic compounds in order that new herbicides may be more intelligently selected and developed for weed control. The data presented are mainly measurements of CO_2 uptake (apparent photosynthesis), CO_2 output (respiration), and dry weight studies under specific conditions.

LITERATURE REVIEW

The diverse uses of 2,4-D as a growth-promoting or growth-inhibiting substance have caused numerous investigators to conduct many studies to evaluate the physiological response of plants when treated with 2,4-D. As a result of such broad and inquiring interest, innumerable reports have been published concerning the effects of 2,4-D and other chemicals on various plant processes.

Shaw, et al. (62), and Shaw and Danielson (63) have emphasized that for the most effective utilization of herbicides it is important to know their nature and properties, sites and mechanisms of action, metabolic fate in plants and soil, and the environmental influence on their performance. It is further pointed out by Shaw and Danielson (63) that herbicides kill weeds by their interference in such vital processes as respiration, photosynthesis, transpiration, and mitosis. As an example, 2-chloro-4,6-bis(ethylamino)-s-triazine (simazine) was listed as being very effective in inhibiting the ability of the chloroplast to function in the photosynthetic process, thereby causing insufficient production of sugar and starch.

Jukes (42) reported that 3-amino-1,2,4-triazole (amitrole) acts as an antimetabolite. He defined a metabolite as "a compound that occurs in living organisms and has an essential function in a biochemical process". The

action of amitrole as an antimetabolite is that of blocking the synthesis of vitamins and chlorophyll. McWhorter and Porter (48) reported that amitrole caused the production of chlorotic tissue in corn plants. In comparing untreated plants to amitrole treated plants they observed a much lower respiratory quotient with the treated plants. The assumption was made that untreated plants metabolized basically carbohydrates, whereas amitrole treated plants metabolized fats as a major respiratory substrate. They also observed that oxygen uptake in chlorotic tissue was inhibited by iodoacetate and malonate as compared to control tissue. Nevertheless, sodium fluoride caused nearly the same degree of inhibition in both tissues. The metabolism of amitrole in different plants was studied by Carter and Naylor (17). They noted that amitrole was metabolized very rapidly in plants from many families. It is suggested that some one or more of the compounds derived from amitrole in plants may possess phytocidal activity.

The fact that many physiological responses of plants to 2,4-D may be of a secondary nature was discussed by Mitchell (50). Among these possible secondary responses are an increase in the moisture content of tissues, hydrolysis of reserve carbohydrates, and depletion of sugars.

Numerous reports (21, 22) have been presented explaining the mechanisms of absorption, translocation, and mode of action of herbicides. The completion of any herbicidal action may involve penetration, absorption by cells, migration to the vascular system, translocation, and a final

toxic action generally involving the living protoplasm. Crafts (22) gives four possible fates of an applied herbicide in regards to penetration: (i) it may remain on the outer leaf surface either in a crystalline or liquid form; (ii) it may penetrate into the cuticle and remain there in solution; (iii) it may proceed into the cuticle and then into the aqueous portion of the epidermal cell walls and it may migrate via the anticlinal walls to the vascular system; and (iv) it may follow the latter route into the leaf and be absorbed into the symplast and then move to the phloem and out of the leaf into the assimilatory stream.

In a previous report Wiese and Rea (75) concluded that phenoxy herbicides are most effective in the control of bindweed when growth conditions are unfavorable. According to their report, temperature and humidity conditions at various times of the day had no effect on 2,4-D toxicity to bindweed. Foy (28) working with 2,2-dichloropropionic (dalapon) emphasized two types of physiological action which he termed acute toxicity and delayed growth regulatory responses.

Baker (7) found that 1,2-dihydropyridazine-3,6-dione (maleic hydrazide) in concentrations of 0.01 M and above inhibited oxygen uptake by tobacco tissues to varying degrees depending upon the pH of the solution. No inhibitory effect on various plant dehydrogenases by maleic hydrazide was observed. However, maleic hydrazide inhibited diaphorase nearly to the same degree as it did respiration. This suggested the possibility of this enzyme being involved in the respiratory process but no proof was provided.

Weinstein (74) pointed out that both increased and decreased respiratory activity have resulted from the treatment of plants with fluoride. He emphasized the view that the effect of fluoride on tissue respiration was largely determined by the amount that reached the active cellular sites and that the conditions of light, temperature, time, etc. played an important role. The data in this report suggested the possibility of an uncoupling of phosphorylation or reduced transphorylation by fluorides or by a product of fluoride metabolism.

Ashton (4) by treating red kidney beans and Kanota oats with 2-chloro-4-ethylamino-6-isopropyl-amino-s-triazine (atrazine) demonstrated that characteristic leaf injury symptoms occurred specifically in light but not in dark. Employing different quantities of tungsten light he noted that less injury appeared with lower light intensity. Reductions in the rate of transpiration by atrazine treatment of soybeans and corn were observed by Smith and Buchholtz (64). These reductions were attributed to stomatal closure after atrazine treatment which indicated the inhibition of water uptake at the stomata. "Stomatal closure after treatment with atrazine would thus appear to be a result of increased CO_2 in the guard cells and substomatal cavities resulting from the inhibition of photosynthesis and increased respiration rate instituted by the herbicide".

Chrispeels and Hanson (18) noted an increase in the ribonucleic acid (RNA) content of soybean hypocotyl treated with 2,4-D. They reported that the increase was more rapid

during the second 24 hour period. More than half of the increased RNA occurred in the microsomal fraction. They proposed that the herbicide renewed nuclear activity leading to the synthesis of RNA and protein, thereby a reversion to meristematic metabolism took place.

Pallas (58) reported that increased temperatures from 20 to 30 C increased absorption and translocation of 2,4-D and benzoic acid by red kidney beans. However, less 2,4-D or benzoic acid was absorbed and translocated at low humidities (34-48%) than at high humidities (70-74%). He correlated the increased absorption and translocation at high humidities with the degree of stomatal opening. Pallas and Williams (59) have stated that the absorption and translocation of 2,4-D and P^{32} were markedly reduced in red kidney bean plants at high moisture tensions. However, soil-moisture stress had no effect on the absorption of 2,4-D and much more was translocated at 1/3-atm than at 4-atm. According to Wedding and Blackman (73) the uptake of 2,4-D by Chlorella may be suppressed in the presence of auxins, particularly, 2,4,5-trichlorophenoxyacetic acid (2,4,5-T), indoleacetic acid (IAA), and 4-chlorophenoxyacetic acid (4-CPA). These workers consider that the depressed uptake of 2,4-D in the presence of 2,4,5-T, IAA, and 4-CPA by Chlorella is of a competitive nature. It is postulated that either compound may replace the other. Williams, Slife, and Hanson (77) found cocklebur was more sensitive to 2,4-D than smartweed, jimson weed or bur cucumber. From the results of their study they concluded that some factors

other than the amount of cellular absorption were responsible for the herbicidal activity in these weeds. The typical 2,4-D epinastic responses in leaves and stems were observed in all five weeds. Although these workers were able to induce injury with low and high concentrations of 2,4-D, complete kill was not effected because 2,4-D failed to be translocated to untreated branches. This was offered as an explanation for incomplete kill of close weed stands.

Wort (78) pointed out that 2,4-D may affect various enzymes in many different ways depending on the plant species, plant part, age, and physiological condition of the plant. Some enzymes are increased where others are decreased.

Lockhart (47) stated that gibberellic acid (GA) was the controlling factor in the regulation of stem growth by visible radiation. He pointed out that any increment in plasticity of the primary cell wall results in a growth increase. Thus, visible irradiation causes a decrease in plasticization resulting in the inhibition of stem growth through a decrease in cell elongation. However, GA or auxin appear to be the necessary growth factors essential for increasing plasticity. It is concluded that visible irradiation somehow reduces the amount of GA.

Employing flax in an intensive study relating the interaction of temperature and light intensity on the effect of 2,4-D, Jordan, Dunham, and Linck (41) demonstrated that the response of flax was affected by light intensity either before or after treatment with 2,4-D. They reported that the

greatest response was with low intensity and least with high intensity. Temperature affected the response of flax to 2,4-D in a somewhat different manner than did light, that is the higher temperature was more effective and the lower less effective. Some interaction occurred between light intensity and temperature. With high light intensity before and after 2,4-D treatment the response of flax at temperatures of 65, 75, and 85 F was quite similar. In the meanwhile, with low light intensity there were large differences in the response of flax to 2,4-D treatment with the above temperatures. The response of flax to 2,4-D under these conditions seemingly showed some unfavorable balance between photosynthesis and respiration.

Jansen, Gentner, and Shaw (40) using corn and soybeans tested 63 surfactants in aqueous spray systems on the effects of the herbicidal activity of dalapon, 2,4-D, amitrole, and 4,6-dinitro-o-sec-butylphenol (DNBP). These surfactants were representative of anionic, cationic, nonionic, ampholytic, and blended-surfactant classes. They noted both suppression and progression of herbicidal activity, as well as no effect. Some surfactants in high concentrations exhibited phytotoxic effects while others stimulated growth at lower concentrations. These workers concluded that the proper selection of surfactants would increase the herbicidal activity of specific herbicides. Thus, the increased efficiency of herbicides would lessen cost and possible damage to desired plants. Gentner and Hilton (30) reported that a 0.3 M sucrose solution reduced

the inhibition of new leaf development of barley plants treated with 3-phenyl-1,1-dimethylurea (fenuron), 3-(p-chlorophenyl)-1,1-dimethylurea (monuron), 3-(3,4-dichlorophenyl)-1,1-dimethylurea (neburon), and 3-(3,4-dichlorophenyl)-1-methylurea (DMU). However, as the concentration of herbicides was increased sucrose became less effective. These investigators thereby claimed that the toxic effect produced by the herbicides was a photosynthate deficiency. They further concluded that the reduced protective effect of sucrose with higher herbicide concentrations indicated the sensitivity of metabolic reactions other than photosynthesis.

Photosynthesis

In a recent review van Overbeek (71) stated that it seems quite conclusive from all available evidence that the urea herbicides interfere with the oxidation of H_2O in the noncyclic photosynthetic electron flow. There appears to be no interference with the reduction of triphospyridine nucleotide (TPN). However, he stated that these herbicides do interfere with the portion of electron flow system which provides low energy electrons to refill the holes in the chlorophyll. These so-called holes come about as a result of photons of light striking the chlorophyll apparatus setting free some electrons which leave behind holes. Thus, if the holes are not refilled and electrons are continually leaving, the chlorophyll eventually becomes oxidized.

The importance of photosynthesis and its relation-

ship to plant growth under natural and artificial conditions as influenced by light, temperature, CO_2, and various other factors is well discussed by several investigators (1, 16, 23, 29, 51, 68). Gaastra (29) emphasizes the implicit relationship between the origination of organic matter and energy from photosynthesis essential for the maintenance of higher plants. Sorokin (65) concluded the upward and downward trends often observed in gas exchange during photosynthesis experiments may be brought about by the building up or activation of some essential participants in the photosynthetic process and as a result of the destruction, consumption, or inactivation of some photosynthetic agents. Decker and Tió (23) compared the amount of photosynthetic work done by leaves of coffee plants to the net gain or dry weight increment. They concluded that the major part of the photosynthetic work was immediately cancelled by photorespiration since the dry weight increment was low. These workers stressed that dry weight increment is directly proportional to the excess of photosynthesis over respiration. It has been found that the leaf polysaccharides are linked to the early products of photosynthetic assimilation of CO_2 (52).

Ormrod (57) found that the photosynthesis of rice plants with low light intensity was not harmed so long as the temperature remained low. However, high temperature with low light intensity for extended durations may have significant effects on CO_2 uptake and output. He concluded that vast losses of carbohydrates could occur resulting in a

dry weight decrease. Yet, the photosynthetic rates of rice plants were not extensively reduced nor was the photosynthetic mechanism injured by low temperature with or without low light intensity. Rhykerd, Langston, and Peterson (61) using three different light treatments for alfalfa, red clover, and birdsfoot trefoil found the uptake of CO_2 by a plant under a specific light environment apparently was affected by the previous light environment in which it had grown. Illumination with a constant light intensity was more favorable for CO_2 uptake than one of the same length and quantity but at several different light intensities. In their experiments CO_2 uptake by birdsfoot trefoil seedlings was lower than that of alfalfa and red clover under all light treatments. Black, Turner, and Gibbs (10) stated that CO_2 assimilation by photosynthesis in plants is dependent on adenosine triphosphate (ATP) and reduced triphosphopyridine nucleotide (TPNH) formation. They observed a lag in CO_2 fixation at low light intensities, whereas increased light intensities resulted in rapid assimilation of CO_2. A similar lagging was observed in ATP formation with low light intensities. Therefore, it was suggested that at low light intensities ATP formation may be a limiting factor in CO_2 fixation by chloroplasts.

It is reported that leaves illuminated with red light generally absorb larger amounts of CO_2 than leaves illuminated with blue light (70). These reporters (70) found that the wavelength of light had no effect on the distribution of absorbed CO_2 between the ethanol-soluble and -insoluble

products of photosynthesis in tobacco leaves.

Berrie (9) supplying tomato plants with an exogenous supply of sucrose found that plants sprayed 10 to 20 times gave the greatest dry weight increment. Little difference was observed whether the sprays were given in the evening, that is, at the end of the illumination period, or in the morning, prior to illumination. Plants sprayed with the sucrose solution were exposed to various temperatures and light intensities under 8 hour day and 16 hour day. In all instances there was nearly a doubling of the total dry weight increment of sucrose sprayed plants over control plants at the end of the 8 hour day experimental period. However, with the 16 hour day only high temperatures and/or low light intensities produced any substantial increase in dry weight of the sucrose sprayed plants over controls. Therefore, day-length is reported to be the most important factor determining the degree of utilization of the applied sucrose. With day-light, gold, and green light qualities no differences between sucrose sprayed and control plants were noticed among the different types of light in the case of the 8 hour day. Nevertheless, under the 16 hour day the plants exposed to green light were generally much smaller, and those illuminated with yellow (gold) light made better use of the applied sugar.

Hayashi (35) reported that there was no significant difference in the photosynthetic activity between gibberellic acid treated and control rice and tomato plants on a unit leaf area basis. Nevertheless, the photosynthetic activity of the whole plants increased 10 to 18% in a period of one week after

the treatment with GA. He concluded that the most reasonable explanation for this increase was "the photosynthetic activity per unit leaf area does not change as the result of the GA treatment; but owing to the increase in leaf area, the photosynthetic activity of the whole plant increases". Similar results were obtained by Alvim (2) who tested red kidney bean seedlings with GA. He observed an increase in the photosynthetic rate which he presumed to be due to the rapid translocation of photosynthates from the leaves to the stem. Both Hayashi (35) and Alvim (2) noted a decrease in root dry weight resulting from treatment with GA.

Petroleum oils have been demonstrated to suppress photosynthesis in the leaves of mustard and parsnip plants (37). The suppression or decline in photosynthesis is attributed to the interference with the CO_2 supply. However, parsnip recovered from treatment with both petroleum naphtha and paraffinic oil, whereas mustard recovered only from treatment with the paraffinic oil.

Certain triazine herbicides may inhibit CO_2 fixation of red kidney bean plants in light according to Ashton, Zweig, and Mason (5), and Zweig and Ashton (79). The degree of inhibition varied with the concentration of the herbicide, increasing with an increased concentration.

The effects of monuron on plant growth have been investigated by several workers (34, 49, 67). Both Minshall (49) and Sweetser and Todd (67) presented data which support the suggestion that monuron interferes with some phase of photosynthesis. Yet, Hassall (34) reported that photosynthetic

conditions had no influence on the growth-retarding effect of monuron. Thus, light has been emphasized as influencing the action of monuron by some investigators while others presume it is ineffective.

Huffaker and Miller (39) reported that in cell-free extracts from bean plants, growth-stimulating concentrations of 2,4-D increased the activity of several enzymes essential for CO_2 fixation. However, the activity of the same enzymes was decreased by growth-inhibiting concentrations of 2,4-D. Wedding and Black (72) found that 2,4-D was effective in inhibiting the incorporation of P^{32} into ATP and adenosine diphosphate (ADP) stimulating oxygen uptake by Chlorella.

Respiration

Recently, Hackett (31) extensively reviewed a large number of reports on the respiratory mechanisms in higher plants. He stated that "respiration, or "life with air", involves the breakdown and oxidations of organic compounds, the transfer of hydrogen (electrons) to molecular oxygen, and the release of utilizable energy within the cell".

Hartman (33) found that post-harvest ripening tomatoes treated with several synthetic growth substances produced more CO_2 than did similar untreated fruits during the ripening period. Thus, it is recognizable that these growth substances caused an increase in the metabolic activity within the fruits. Yet, CO_2 evolution from freshly harvested asparagus spears was shown to be inhibited by post-harvest application of N^6-benzyladenine (24). Norris and Foulds (56)

reported that GA in concentrations of 1 to 200 ppm had no significant effect on the oxygen uptake of onion root tips whereas IAA in concentrations of 10, 50, and 100 ppm caused inhibition of oxygen consumption of the apical segment of onion roots.

Farkas, Konrad, and Kiraly (26) found that illumination of etiolated wheat seedlings increased their sensitivity to malonate, a specific and potent inhibitor of succinic dehydrogenase. Such inhibitory action could bring about an interference in the rate of respiration. Green seedlings previously illuminated exhibited an increased respiratory rate. Both stimulatory and inhibitory effects were observed as a result of treating mustard and parsnip plants with various petroleum oils (36).

According to Applegate, Adams, and Carriker (3) fluoride solutions, depending on the concentration, promoted or inhibited oxygen uptake of intact bush beans. In contrast, Hill, et al. (38) noted that fluoride had no effect on the respiration of seven species of plants with either low or high fluoride concentrations.

The effects of 2,4-D on respiration in plants have been discussed by Klingman (45). He stressed that the rate of respiration may either be stimulated or retarded by 2,4-D. The threshold concentration which may cause an increase or inhibition in CO_2 output depends upon the plants' tolerance to 2,4-D. Generally, low concentrations are assumed to stimulate, where high concentrations are observed to inhibit

respiration. 2,4-D is reported to cause closure of the plant's stomates, which causes reduction in the CO_2 uptake and output. Black and Humphreys (11) reported that etiolated corn seedlings treated with 2,4-D prior to the preparation of cell-free extracts resulted in a general increase of enzymic activity associated with the pentose phosphate cycle. They found an increased utilization of ribose-5-phosphate and 6-phosphogluconate in cell-free extracts from 2,4-D treated corn seedlings. They concluded that 2,4-D treatment of etiolated corn seedlings affected glucose catabolism as a result of an increase in the amount catabolized via the pentose phosphate cycle.

Photosynthesis and Respiration

Brix (14) studied the effect of water stress on the rates of photosynthesis and respiration by tomato plants and loblolly pine seedlings. He observed decreases in the rates of photosynthesis and respiration with increasing water stress which he related to the diffusion pressure deficit. He also found similar changes in the rates of transpiration and photosynthesis during increasing water stress indicating that photosynthesis was affected by an increased resistance to gaseous diffusion. Moss, Musgrave, and Lemon (53) tested the effects of several environmental factors on photosynthesis, respiration, and transpiration of corn. They reported that the intensity of solar radiation was the predominant factor affecting the rate of photosynthesis. With increased CO_2

concentrations about the plants they noted an increase in assimilation, particularly with high light intensity. Increasing night temperatures caused increased respiratory activity. These workers also noticed a reduced rate of assimilation with water stress conditions.

Gibberellic acid was observed to cause a rapid increase in the rates of respiration, photosynthesis, and transpiration (20). After a maximum rate was reached a sudden decline took place. The rate of transpiration returned to its initial whereas that of respiration and photosynthesis of the treated plants remained higher than that of untreated plants. Kandler (43) reported that 2,4-dinitrophenol (DNP) in concentrations which inhibited oxidative phosphorylation and increased respiration did not inhibit photosynthesis.

Nieman (55) working with 12 crop plants found that NaCl did not appreciably suppress the photosynthetic activity of leaf samples on an unit area basis. On the other hand, respiration was slightly increased in both tolerant and sensitive species. The growth, in general, ranged from stimulated to severely depressed depending on the sensitivity of the plants to NaCl.

The sodium salt of 2,4-D is reported to have a specific effect on the photosynthetic and respiratory processes of plants (60). It is pointed out by these workers (60) that the herbicide causes a suppression of photosynthesis and respiration as well as some stimulation depending on the dosage of the chemical preparation.

MATERIALS AND METHODS

Experimental Growth Room and Equipment

The growth room utilized in this study is a concrete basement, except for the ceiling, located below the ground level under the plant physiology laboratory in the greenhouse.

Temperature and lights are automatically controlled by time clocks giving a temperature of 21 C during the photoperiod (16 hrs) and 16 C during the dark period (8 hrs). Daily temperature cycles are maintained by a Westinghouse Unitaire. A thermograph centrally located provides a continuous temperature record. Although the room is without humidity control this did not vary significantly from one day to the next because of the continuous air-conditioning.

Light sources. Fluorescent lamps of two types were used in this study. General Electric 96-inch T-8 slimline fluorescent lamps in warm white, cool white, blue, green, yellow (gold), pink, and red were used. Also, Sylvania Electric 96-inch T-12 Very High Output (VHO) fluorescent lamps in warm white, cool white, blue, and red were used. The spectral distribution curves of these lamps may be seen in Figures 1 and 2. See Table 1 for the various symbols used to designate the different lamps.

Measurement of the light intensity. Light intensity was measured in foot-candles and microwatts per square centimeter using a General Electric multi-cell light meter and an Eppley thermopile connected to a Kintel Electronic Galvanometer,

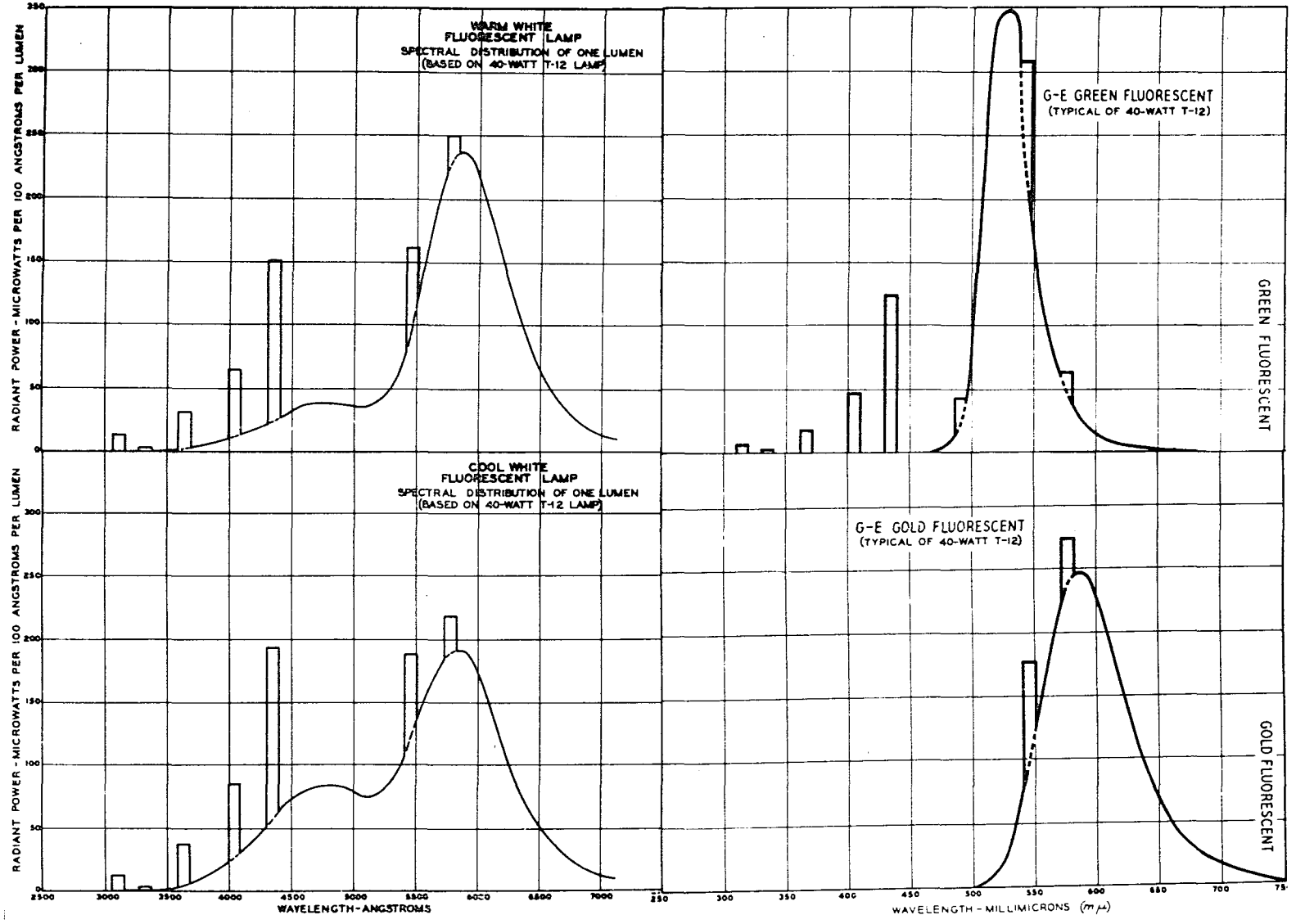

Fig. 1. Spectral distribution curves for General Electric fluorescent lamps.

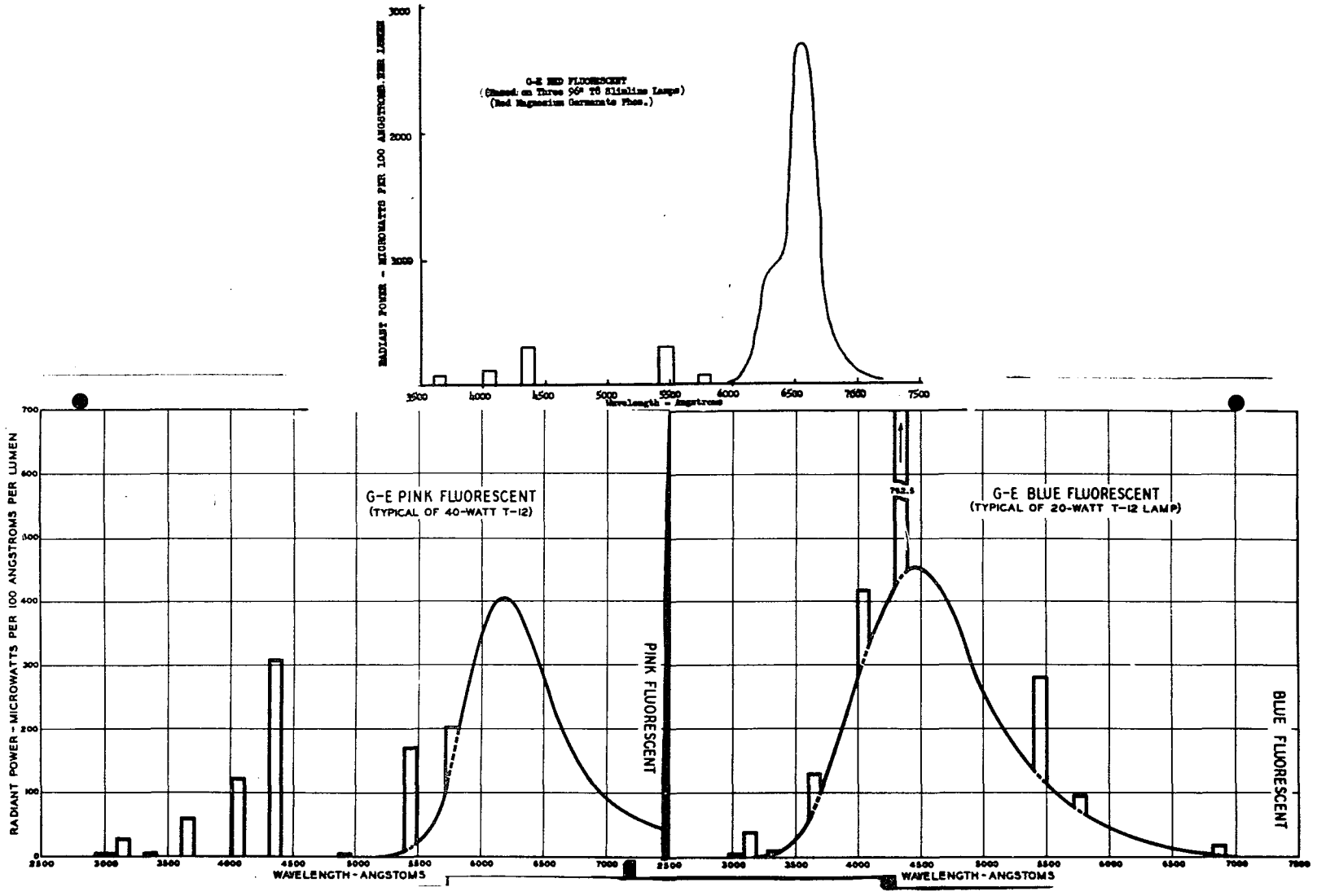

Fig. 1. -- Continued.

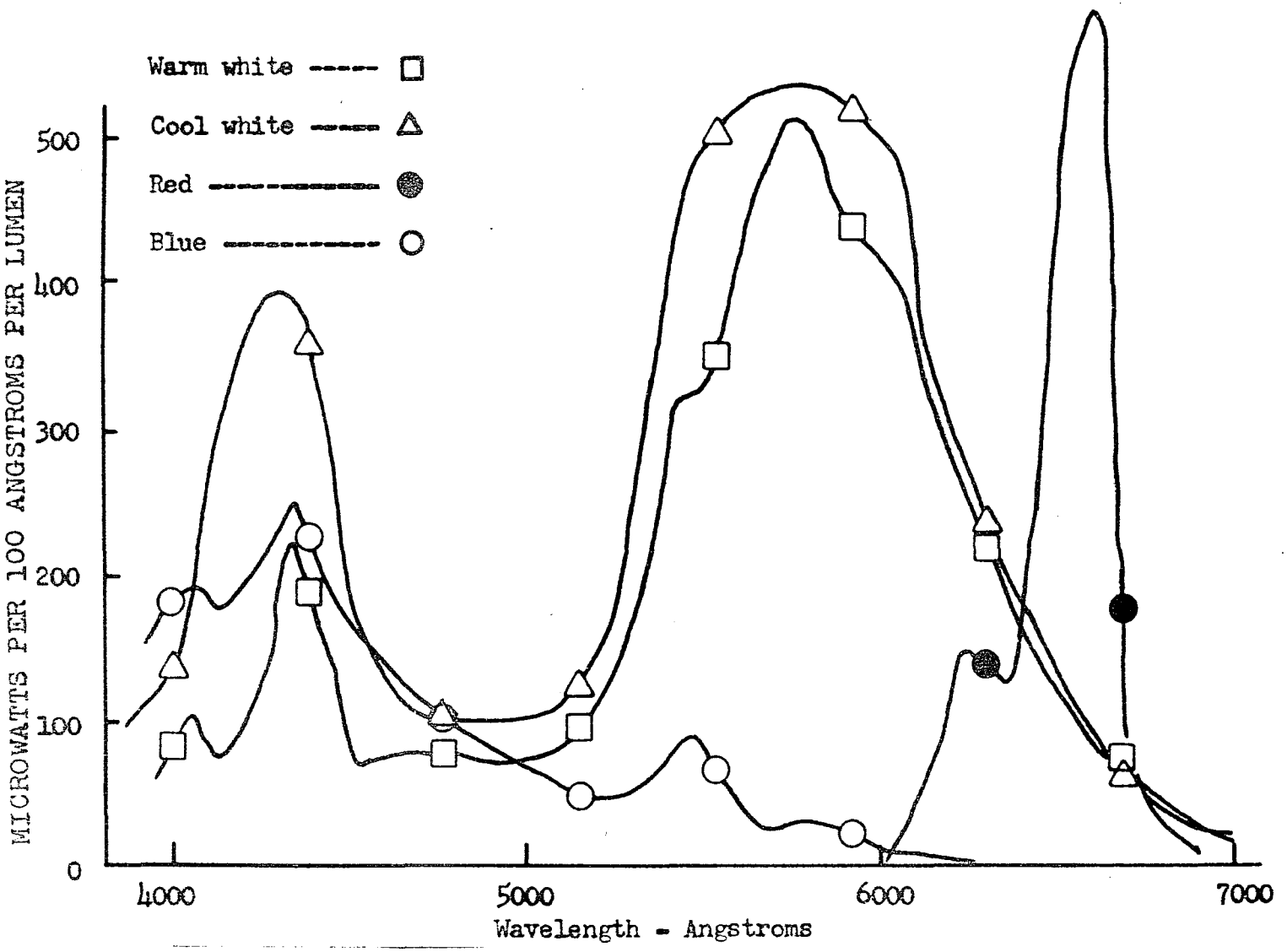

Fig. 2. Spectral distribution curves for Sylvania Electric fluorescent lamps.

Table 1. Symbols used

Symbol	Explanation
	General Electric Lamps
W	Warm white fluorescent lamp
CW	Cool white fluorescent lamp
B	Blue fluorescent lamp
Y	Green fluorescent lamp
P	Pink fluorescent lamp
R	Red fluorescent lamp
	Sylvania Electric Lamps
VW	VHO warm white fluorescent lamp
VCW	VHO cool white fluorescent lamp
VB	VHO blue fluorescent lamp
VR	VHO red fluorescent lamp
	Miscellaneous
LSR*	Least significant range at 5% level
ft-c	Foot-candle
$\mu w/cm^2$	Microwatt per square centimeter
p:	Number of means

respectively. However, for high intensities in foot-candles a Spectra Professional exposure light meter was used. The light intensities used were measured as the incident light intensity upon the plant at the beginning of any light treatment. Intensity readings in foot-candles were corrected using the correction factors shown in Table 2 for each light quality used. Thus, the corrected light intensities were the meter readings multiplied by the correction factors. Intensity readings in microwatts per square centimeter were first taken in microvolts and converted to microwatts per square centimeter by dividing by the factor, 0.05 $\mu v/\mu w/cm^2$.

Experimental set-up for testing light effects. A wooden frame consisting of three similar compartments separated by white plastic curtains was used to measure the effects of different light qualities (Fig. 3). Six circular rotating tables were located in each compartment. A neoprene belt, which went around the base of the tables to provide rotation, was run by a 1/3 hp electric motor coupled to a gear reducer which reduced the speed of revolution to 8-10 rpm. Rotation was solely to minimize any positional effects and provide equal distribution of illumination on the plants.

An adjustable luminaire was suspended with ropes and pulleys above the row of rotating tables in each compartment. Each luminaire could hold from 1 to 6 fluorescent lamps, the number depending on the desired light intensity to be used.

Experimental set-up for measuring CO_2 exchange. The CO_2 exchange measurements were made with a Liston-Becker In-

Table 2. Correction Factors

Light quality	Factors
Warm white	1.13
Cool white	1.00
Blue	0.46
Green	1.45
Yellow (Gold)	1.33
Pink	0.94
Red	0.58
VHO warm white	1.13
VHO cool white	1.00
VHO blue	0.99
VHO red	0.89

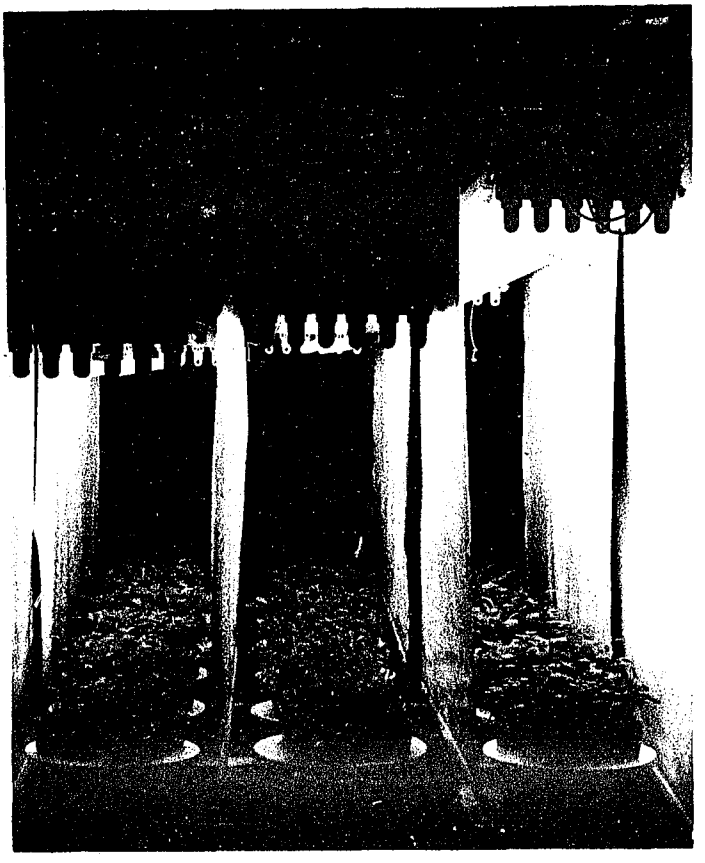

Fig. 3. Experimental set-up for testing light effects.

frared Analyzer Model 15A incorporated in a closed system. The importance of a closed system for studying assimilation and respiration was emphasized in 1926 by Bolas (13). Numerous investigators (12, 15, 46, 54) have used infrared analyzers to measure CO_2 exchange for determining photosynthetic and respiratory activities of plants and plant parts. The experimental set-up for these experiments consists of an L/B Infrared Analyzer (Amplifier and Analyzer), Esterline-Angus Recorder, Brooks Sho-Rate "50" flow meter, Dyna-Pump, and a plexiglas plant chamber (Fig. 4). Also tanks of gas (prepurified N_2 and CO_2 blended in prepurified N_2) of known concentration were connected in the set-up, which could be opened and closed for calibration and for increasing or decreasing the concentration of CO_2 in the system when necessary. Tygon tubing was used to connect the parts of the closed system. Air was circulated in the closed system by the Dyna-Pump at a rate of 4 cubic feet per hour. Figure 5 shows a close up view of the plexiglas plant chamber with a container of 20 plants enclosed in a test run. Whenever measuring the CO_2 exchange the top of the chamber was sealed with Dow Corning high vacuum grease and clamped across each end, thus providing an airtight plant chamber. Inside dimensions of the chamber are 23.5 x 13.3 x 14.3 cm, thus having a volume of approximately 4.5 liters. It could hold one or two containers of plants.

Descriptions and operation procedures of the Infrared Analyzer are outlined in the Beckman Instruction Manual (8).

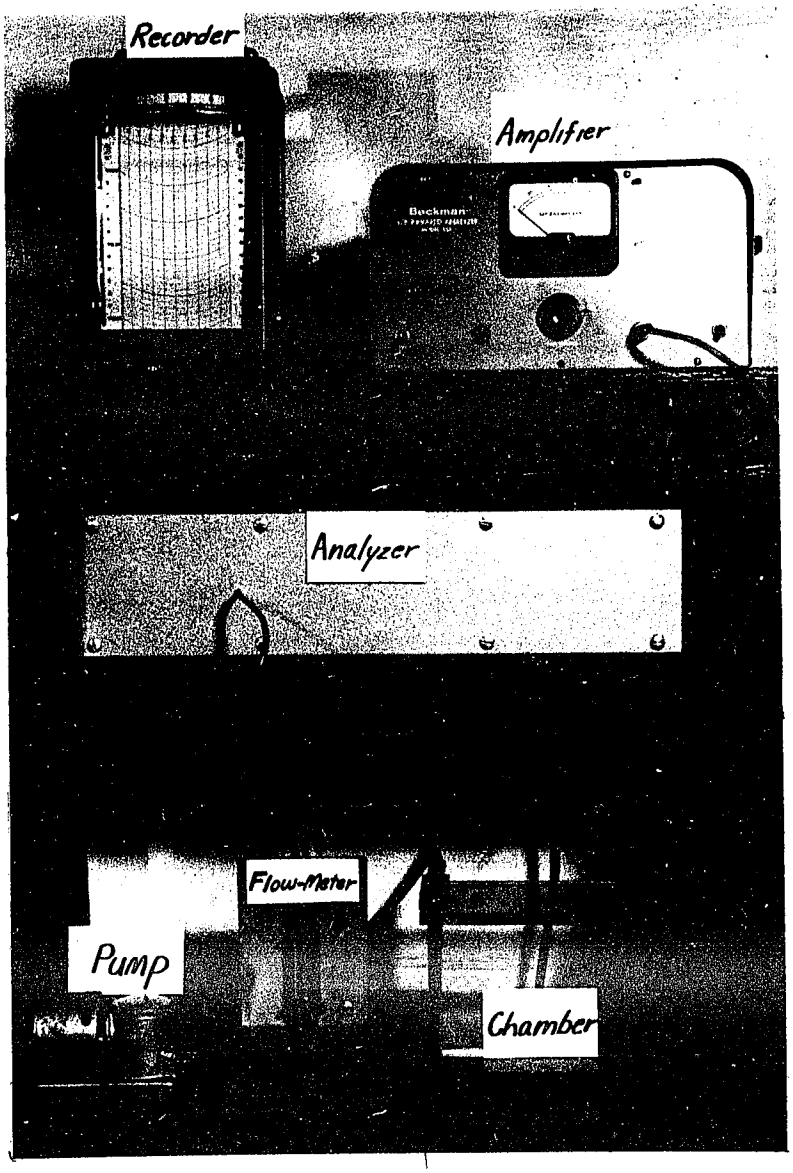

Fig. 4. CO_2 exchange measuring set-up.

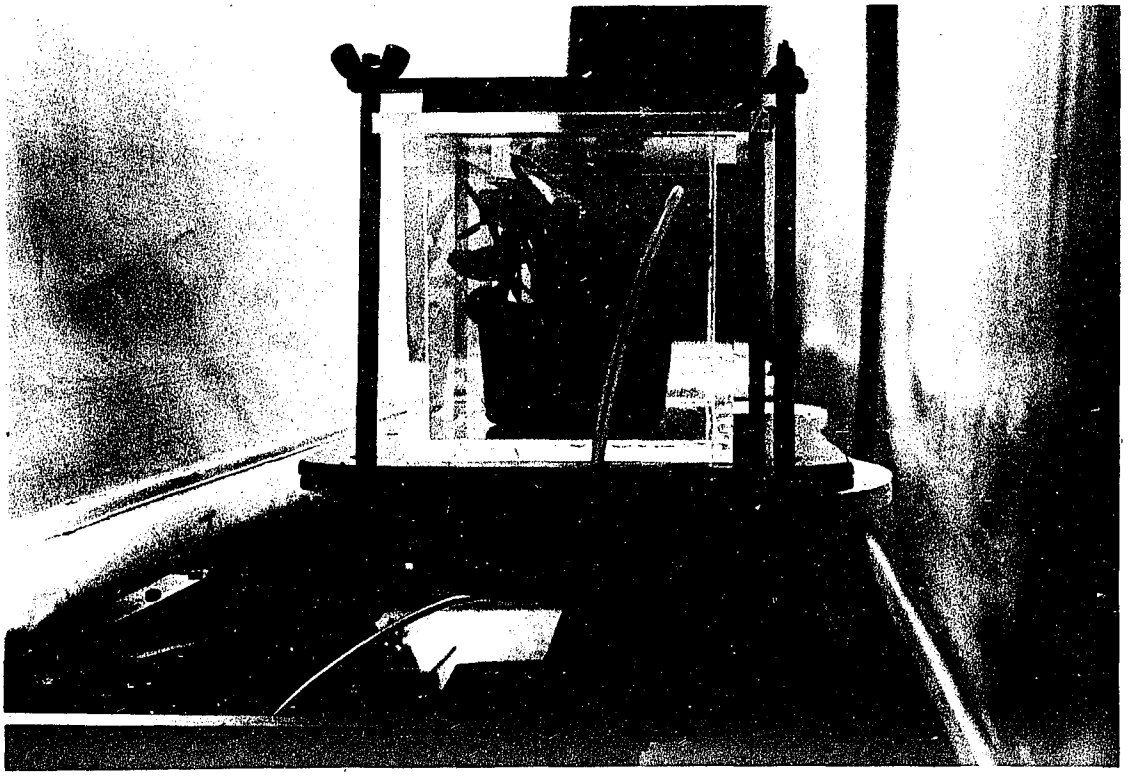

Fig. 5. Plastic plant chamber used in measuring CO_2 uptake and output.

Figure 6 shows a diagrammatic view of the analyzer portion of the L/B Infrared Analyzer. As seen in the figure, the analyzer consists of two infrared radiation sources, an energy beam chopper, sample cell with CO_2 present, reference cell, and a detector with a sensitive diaphragm. Equal amounts of infrared energy are emitted from both radiation sources, which are interrupted by the chopper. One beam of infrared energy passes through the reference cell while the other beam passes through the sample cell. The gas (CO_2 in these experiments) in the sample cell absorbs some of the infrared energy. No absorption takes place in the reference cell, which is filled with N_2. As a result, unequal beams of infrared energy emerge, striking the detector, which consists of two chambers filled with CO_2 at equal pressures. The two chambers are separated by a sensitive diaphragm. When unequal beams of energy strike the detector unequal pressures are produced in the chambers. The diaphragm moves in the direction of the chamber with the lesser pressure. The movement of the diaphragm produces an electrical output signal which is sent to the amplifier. The amplifier contains the operating controls.

General Procedures

Experimental plants. All plants were obtained from seeds of mustard (Brassica juncea (L.) Coss. cultivar Florida Broadleaf) carefully sown in polyethylene containers (1 pint) filled with vermiculite. Each container had four perforations in the bottom for drainage. A sufficient number of seeds

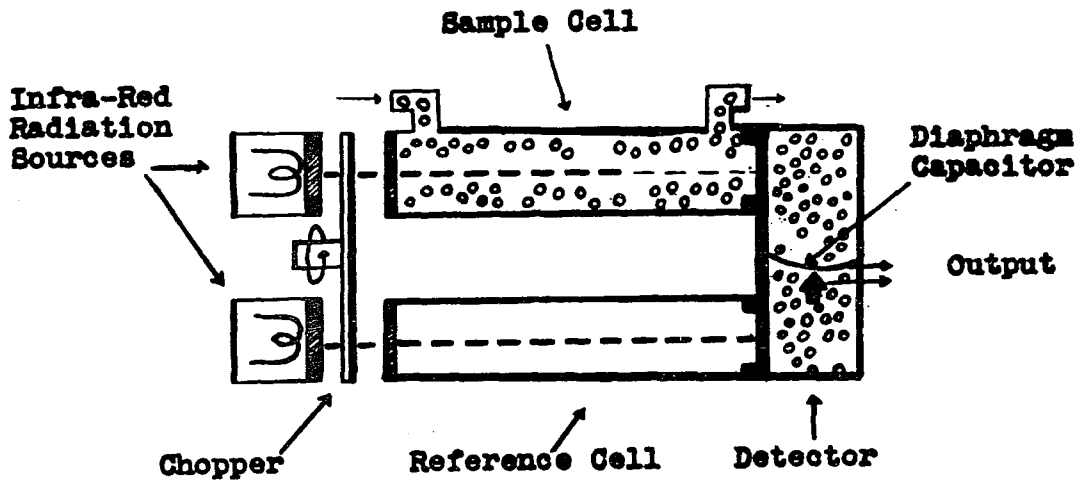

Fig. 6. Diagram of infrared carbon dioxide analyzer.

were sown to obtain 20 plants per container after thinning. Sowing was done at intervals since all plants could not be transferred to the lights at one time. This was done because when measuring CO_2 exchange the time required to do so would not permit all tests to be completed in one day. However, for dry weight studies all seeds were sown at one time for any one experiment.

Nutrition. A modification of Hoagland's nutrient solution (Table 3) was used to provide proper nutrients for the plants. The nutrient solution was applied to the surface of the vermiculite 17 days from sowing and thereafter every 4 days in 40 ml portions per container. The plants were watered with tap water as needed to maintain a moist medium.

Light treatment. The plants were grown in the greenhouse under natural daylight conditions until transferred to the experimental growth room for a particular light quality treatment. Two different light conditioning treatments were used. One is referred to as "short-term light" and a second as "long-term light". With the short-term light the plants were grown in the greenhouse for 32 days and under the light qualities for 5 days, while the plants for the long-term light were grown in the greenhouse for 17 days and under the light qualities for 20 days. Sufficient containers of plants were placed under each light quality to have six replications of any one treatment used in an experiment. That is, one replication of each treatment was placed on all six rotating tables under any particular light quality.

Table 3. Nutrient Solution*

Major elements: Weights in grams for one liter of nutrient solution.

$Ca(NO_3)_2 \cdot 4H_2O$	1.180
KNO_3	0.510
$MgSO_4 \cdot 7H_2O$	0.490
KH_2PO_4	0.140

Minor elements: Weights in grams for a one liter "stock" solution, from which one ml is used for each liter of nutrient solution.

H_3BO_3	2.900
$MnCl_2 \cdot 4H_2O$	1.800
$ZnSO_4 \cdot 7H_2O$	0.220
$CuSO_4 \cdot 5H_2O$	0.080
$H_2MoO_4 \cdot H_2O$	0.020

Iron: One ml of a 0.5% "stock" solution of Dow Versenol F (Iron Sodium N-Hydroxyethylethylene diamine tri-acetate) is used for each liter of nutrient solution.

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* Modification of Hoagland's nutrient solution (27).

Herbicidal treatment. At the end of the light treatment (light conditioning, whether 5 or 20 days) the plants were approximately 8 to 10 cm in height and still in the vegetative stage of growth. Solutions of the sodium salt of 2,4-D (hereafter referred to as 2,4-D) were applied as a fine mist from a hand sprayer, to thoroughly cover the foliage of the plants. In some instances sucrose was mixed with 2,4-D and applied to the foliage, while in other instances sucrose solutions alone were applied. For CO_2 exchange measurements all plants were not treated at one time. Instead, the containers of plants were treated at intervals to allow a 24 hour post-spray period under the lights before measuring the CO_2 exchange. For dry weight studies all plants were treated at one time and given a post-spray period of 10 days under the lights. The various solutions were applied to the plants outside the experimental growth room. After the plants had dried they were returned to their original position under the lights.

CO_2 analyses. As pointed out under "Experimental set-up for measuring CO_2 exchange" an Infrared Analyzer was used to measure the changes in CO_2 concentration. Prior to measurement of CO_2 output and uptake the Infrared Analyzer was calibrated with gases of known concentration. However, before calibration the entire analyzer was warmed-up over night in the experimental growth room with all switches in the "on" position. N_2 was used to obtain the zero point on the recorder and 600 ppm of CO_2 was used to obtain the 100 point (full scale) on the recorder. In calibrating, the

"closed system" was left open and the gas allowed to flow through at a rate of 4 cubic feet per hour. Both the zero and 100 points were rechecked several times to correct for any drift that might have occurred during the process of calibrating. After this, two lower concentration of CO_2 (300 and 500 ppm) were used to obtain two intermediate points. A calibration curve was drawn based on these four points (0, 65, 91, 100, recorder deflection) obtained on the recorder from which the concentration of CO_2 in the range of 0 to 600 ppm could easily be read.

After the instrument was calibrated a container of 20 plants was sealed in the plant chamber (See Fig. 5). In measuring CO_2 output (respiration) N_2 was flushed through the system to reduce the level of CO_2 in the system to 170 ppm. This level was chosen because it represented the compensation point under these experimental conditions. Upon reaching 170 ppm the N_2 was cut-off, the system closed and the Dyna-Pump started. Immediately the lights were switched-off and CO_2 output measured for one hour. At the end of this period CO_2 concentration was raised or lowered to 500 ppm and the lights switched-on permitting CO_2 uptake for an hour. This was repeated for a container of treated plants and a container of control plants for each of the six positions under all the different lights used.

The lines on the recorder charts for the divisions of time are curved, thus points for each ten minutes are read and replotted on straight--line graph paper (20 squares per

inch) in terms of ppm based on the calibration curve. Figure 7 shows a typical set of curves for warm white light. The areas a and b shown in Figure 7 are regarded as the 2,4-D effect as influenced by light quality upon respiration and apparent photosynthesis respectively. These areas were measured in square centimeters with a polar planimeter and converted to microliters of CO_2. This was done for six replications in each treatment of an experiment.

Dry weight analyses. After the plants of various treatments had been subjected to the specific light conditions for the required pre- and post-spray periods, the tops of the 20 plants per container were harvested and dried for 10 days at 50 C in a drying oven, then the dry weight was determined. There were six replications in each experiment for all treatments, except in one experiment in which there were twelve replicates. Representative samples of the plants were harvested at the beginning of the light treatments and the mean dry weight determined and later subtracted from the dry weight of each replicate in the experiment. Therefore, the values given represent the dry weight increase of each replicate. However, some values shown represent differences between specific treatments.

Statistical evaluation of the effectiveness of light qualities. The differences in CO_2 uptake and output between control and treated plants in microliters were subjected to analysis of variance as outlined by Steel and Torrie (66), and Duncan's (25) multiple range test applied using the critical

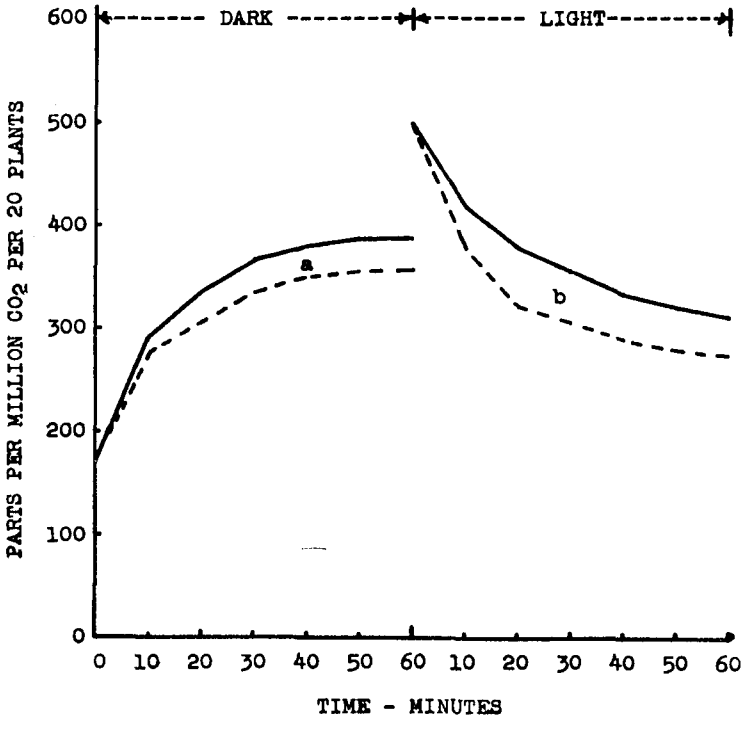

Fig. 7. Typical curves showing the effect of warm white light at 600 $\mu w/cm^2$ on CO_2 exchange (---- Control; ——— Treated).

values suggested by Harter (32).

The suggestions presented in the style manual for biological journals (19) were followed in the preparation of this manuscript.

RESULTS AND DISCUSSION

Effects of Light Quality and 2,4-D on Photosynthesis and Respiration

It is evident from the curves in Fig. 8 that with extended post-spray periods 2,4-D increasingly suppresses CO_2 uptake and promotes CO_2 output by mustard plants grown under the experimental conditions described earlier in the materials and methods. The slope and magnitude of the curves showing CO_2 uptake and output by mustards depend greatly upon the concentration of 2,4-D and light treatment.

Although results obtained using different light intensities are presented in the data, the main emphasis is placed on the effect of different light qualities. Nevertheless, comparisons are made between light intensity measured in foot-candles and microwatts per square centimeter. Such comparison is of particular interest because recent advances in phytoillumination stress the importance of light measurements in incident energy and not illuminance, especially so when comparing various light colors.

Plants used as controls and test plants (treated) were selected for uniformity of size, age, and appearance. From the data reported it is evident that in many instances considerable variability exists between replications for any one light treatment under the conditions of the experiment. In fact, some of the differences between replicates exceeded the differences between the means for light qualities.

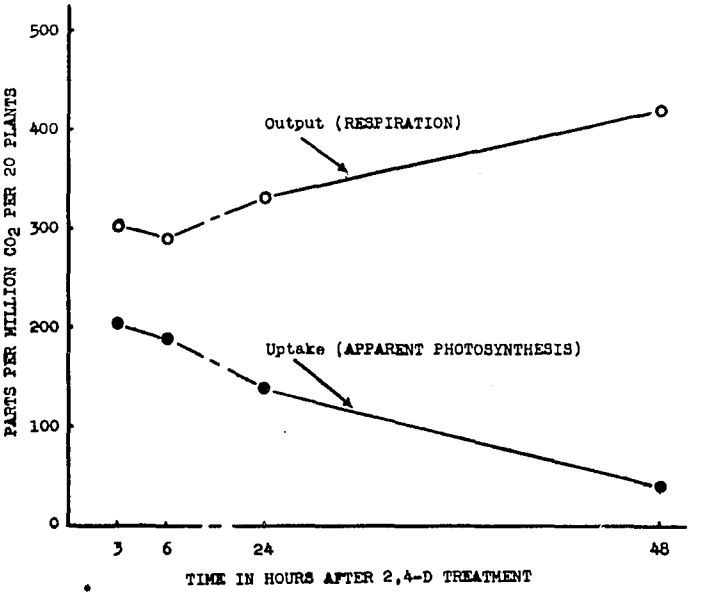

Fig. 8. Effect of short-term warm white light at 600 $\mu w/cm^2$ on the action of 2,4-D on CO_2 exchange by mustard plants with different post-spray periods.

According to the procedure (see Materials and Methods) used to collect the data some variability were expected. In statistical analyses of the data presented below no correction was established for the variability in replication. Thus it is possible that if some modification of the method of analysis had been established to correct for variability between replicates more significant differences might have been observed among light qualities.

Low light intensity and 100 ppm 2,4-D. Experiments were designed to test the effects on photosynthesis and respiration of light quality using low light intensity measured in foot-candles and 100 ppm 2,4-D. Short-term and long-term light conditioning were used in these experiments. Results are shown in Tables 4 and 5. These results indicate that there are generally no really significant differences among light qualities in modifying the effects of 2,4-D, at such low concentration, either on CO_2 uptake or output. However, with short-term light condition the effect of blue was significant over pink at the 5% level.

Differences between mean microliters of CO_2 output for different light qualities (Tables 4, B and 5, B) for short-term light conditioning are much less than those for the long-term light conditioning. Apparently the short-term light eliminates some of the sharp differences among light qualities found when using long-term light. More morphological differences of plants occurred under light qualities with long-term light. Plants illuminated with blue, and red light are usually short and stalky with rather thick leathery leaves.

Table 4. Effects of short-term (5 days) light at 300 ft-c and 100 ppm 2,4-D on photosynthesis and respiration by mustard plants.

A. "Apparent Photosynthesis"- Differences in CO_2 uptake between control and treated plants (20 plants each) in microliters for one hour.

W	B	G	Y	P	R
118	143	37	174	46	174
125	132	113	72	65	97
79	190	118	102	58	106
118	136	150	26	48	95
48	97	88	48	148	132
102	97	28	72	26	67
Mean 98	132	89	82	65	112

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	49	51	53	54	55

Lights:	P	Y	G	W	R	B
Means:	65	82	89	98	112	132

B. "Respiration"- Differences in CO_2 output between control and treated plants (20 plants each) in microliters for one hour.

W	B	G	Y	P	R
113	14	83	58	42	109
32	132	18	14	76	46
30	194	23	35	79	62
176	23	124	25	144	23
18	58	162	21	2	30
95	25	14	124	35	35
Mean 77	74	71	46	63	51

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	69	73	75	76	78

Lights:	Y	R	P	G	B	W
Means:	46	51	63	71	74	77

*Least significant range at the 5% level.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.

Table 5. Effects of long-term (20 days) light at 300 ft-c and 100 ppm 2,4-D on photosynthesis and respiration by mustard plants.

A. "Apparent Photosynthesis"- Differences in CO2 uptake between control and treated plants (20 plants each) in microliters for one hour.

W	B	G	Y	P	R
146	234	155	81	160	53
56	102	16	100	183	162
162	185	92	67	178	171
160	86	92	109	169	37
86	134	125	132	139	67
384	164	48	21	92	74
Mean 166	151	88	85	154	94

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	81	85	88	90	91

Lights:	Y	G	R	B	P	W
Means:	85	88	94	151	154	166

B. "Respiration"- Differences in CO_2 output between control and treated plants (20 plants each) in microliters for one hour.

W	B	G	Y	P	R
269	162	142	98	14	81
12	127	39	28	160	415
167	44	67	127	90	231
99	90	84	58	34	42
106	317	162	100	76	58
51	25	21	16	178	34
Mean 117	128	86	71	92	144

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	112	118	121	124	126

Lights:	Y	G	P	W	B	R
Means:	71	86	92	117	128	144

*Least significant range at the 5% level.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.

A similar type of plant response is observed with plants illuminated with pink, and warm white light but to a lesser degree than that of plants under blue, and red. Green, and yellow usually cause an attenuation in stems and leaf blades. Also the leaves are thin as compared to leaves of plants grown under blue, red, pink, and white lights. Thereby, the long-term light is presumed to be the main factor in causing large differences in CO_2 uptake among different light colors.

Low light intensity and 500 ppm 2,4-D. To evaluate the effects of light quality on the 2,4-D effect, several experiments were conducted using an increased concentration (500 ppm) of 2,4-D. In one experiment light intensity was 600 $\mu w/cm^2$ with short-term light conditioning. Table 6 shows the results of gas exchange measurements made in this experiment. Among light qualities the interference of pink light with CO_2 uptake by 2,4-D treated plants over control plants was statistically significant at the 5% level above warm white, blue, and green. Although non-significant, the differences between yellow, red, and pink were appreciably large (Table 6, A). At the 1% level the effects of pink light were significant over warm white in causing 2,4-D to inhibit CO_2 uptake.

The respiratory process was stimulated by 2,4-D under each light quality. Nevertheless, there were no significant differences in CO_2 output among light qualities (Table 6, B).

In a second experiment the light intensity was 300 ft-c using long-term light conditioning. Results of this ex-

Table 6. Effects of short-term (5 days) light at 600 $\mu w/cm^2$ and 500 ppm 2,4-D on photosynthesis and respiration by mustard plants.

A. "Apparent Photosynthesis"- Differences in CO_2 uptake between control and treated plants (20 plants each) in microliters for one hour.

	W	B	G	Y	P	R
	227	185	183	245	660	317
	109	142	250	150	123	155
	27	262	204	109	380	26
	139	44	46	174	504	570
	39	50	232	37	176	58
	178	262	123	479	322	218
Mean	120	158	173	199	361	224

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	159	167	173	176	179

Lights:	W	B	G	Y	R	P
Means:	120	158	173	199	224	361

B. "Respiration"- Differences in CO_2 output between control and treated plants (20 plants each) in microliters for one hour.

	W	B	G	Y	P	R
	95	248	111	232	328	319
	65	65	187	17	86	148
	185	139	171	106	131	65
	127	41	276	216	301	400
	350	287	97	257	88	72
	61	39	264	564	294	155
Mean	147	136	184	232	205	193

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	147	154	160	163	165

Lights:	B	W	G	R	P	Y
Means:	136	147	184	193	205	232

*Least significant range at the 5% level.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.

periment are presented in Table 7. As seen in part A of Table 7, warm white, and blue light reduced the CO_2 uptake in 2,4-D treated plants, as compared to control plants, to a greater extent at the 5% level than yellow and pink. Green was significant over yellow in its effect on the inhibition of apparent photosynthesis by 2,4-D. White was significantly effective at the 1% level over yellow in modifying the effect of 2,4-D in CO_2 assimilation.

Among light qualities, only red showed any significance in the promotion of CO_2 output. Thus, red was significant at the 5% level above pink. This type of difference between red and pink is unexpected since pink has a great deal of red in its spectral makeup (see Fig. 1, Spectral Distribution curves for pink and red lamps).

From the results of these experiments it is apparent that certain aspects of the 2,4-D effect on photosynthesis and respiration are extended more with the long-term light conditioning than with the short-term light conditioning.

Low light intensity and 1000 ppm 2,4-D. Two experimental tests were performed to determine the effect of light quality on the action of 1000 ppm 2,4-D. The short-term light conditioning period was used in each experimental test. The intensity in the first experiment was 600 $\mu w/cm^2$. Results (Table 8, A) of CO_2 uptake measurements based on the difference between 2,4-D treated and control plants exhibited no statistically significant differences among light qualities. Although non-significant, warm white and red light caused

Table 7. Effects of long-term (20 days) light at 300 ft-c and 500 ppm 2,4-D on photosynthesis and respiration by mustard plants.

A. "Apparent Photosynthesis"- Differences in CO_2 uptake between control and treated plants (20 plants each) in microliters for one hour.

W	B	G	Y	P	R
148	243	451	70	108	310
445	497	124	93	120	376
556	213	265	102	182	97
335	428	222	209	190	312
447	259	81	58	145	185
145	278	523	82	58	128
Mean 346	320	277	102	134	235

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	153	161	166	170	172

Lights:	Y	P	R	G	B	W
Means:	102	134	235	277	320	346

B. "Respiration"- Differnaces in CO_2 output between control and treated plants (20 plants each) in microliters for one hour.

W	B	G	Y	P	R
122	176	166	63	21	155
297	178	15	93	139	58
193	102	217	74	65	333
223	30	157	181	39	127
202	70	153	139	29	127
69	107	433	65	161	529
Mean 184	110	190	102	76	222

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	124	130	135	137	139

Lights:	P	Y	B	W	G	R
Means:	76	102	110	184	190	222

*Least significant range at the 5% level.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.

Table 8. Effects of short-term (5 days) light at 600 $\mu w/cm^2$ and 1000 ppm 2,4-D on photosynthesis and respiration by mustard plants.

A. "Apparent Photosynthesis"- Differences in CO_2 uptake between control and treated plants (20 plants each) in microliters for one hour.

	W	B	G	Y	P	R
	231	169	199	76	194	171
	146	197	148	255	46	192
	373	95	130	141	245	222
	60	132	167	301	206	118
	306	130	32	259	197	241
	313	35	106	81	224	268
Mean	238	126	130	186	185	202

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	101	106	110	112	114

Lights:	B	G	P	Y	R	W
Means:	126	130	185	186	202	238

B. "Respiration"- Differences in CO_2 output between control and treated plants (20 plants each) in microliters for one hour.

	W	B	G	Y	P	R
	51	60	198	155	58	171
	25	32	139	42	46	192
	280	90	116	125	174	222
	432	53	116	157	107	118
	159	37	35	53	25	242
	148	86	23	78	65	268
Mean	182	60	104	102	79	202

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	89	94	97	99	100

Lights:	B	P	Y	G	W	R
Means:	60	79	102	104	182	202

*Least significant range at the 5% level.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.

greater interference in CO_2 uptake by 2,4-D than any of the other light qualities used.

Red was found to be significantly more effective in promoting a 2,4-D stimulatory effect on respiration above blue, pink, yellow, and green at the 5% level. Warm white was significant over blue and pink in promoting respiration by 2,4-D at the 5% level. Red irradiation was also significant at the 1% level over blue in its promotive effect (Table 8, B).

The light intensity in the second test was 300 ft-c. Blue was markedly effective in causing a reduction in CO_2 uptake in 2,4-D treated plants. At the 5% level blue was significant over all light qualities except pink. Both pink and red were significant over green, yellow, and warm white in inhibitory effects on photosynthesis (Table 9, A). Differences in CO_2 uptake between 2,4-D treated and control plants were significantly influenced by blue over green, yellow, and warm white at the 1% level. Pink and red were significant over green and yellow light.

No significant differences were observed among light qualities in their effect on the differences in CO_2 output between 2,4-D treated and control plants (Table 9, B).

The influence of blue light at low intensity in promoting the interference of 1000 ppm 2,4-D with CO_2 uptake was presented in an earlier report (76). However, in those studies long-term light conditioning periods were used. Blue was found to be highly significant compared to all other

Table 9. Effects of short-term (5 days) light at 300 ft-c and 1000 ppm 2,4-D on photosynthesis and respiration by mustard plants.

A. "Apparent Photosynthesis"- Differences in CO_2 uptake between control and treated plants (20 plants each) in microliters for one hour.

W	B	G	Y	P	R
46	220	185	114	231	319
185	523	123	155	160	136
30	300	32	14	282	127
174	386	60	123	215	252
141	211	69	18	231	222
125	250	12	65	303	245
Mean 117	315	80	82	237	217

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	89	94	96	98	100

Lights:	G	Y	W	R	P	B
Means:	80	82	117	217	237	315

B. "Respiration"- Differences in CO_2 output between control and treated plants (20 plants each) in microliters for one hour.

W	B	G	Y	P	R
208	76	215	92	48	39
116	28	60	92	62	0
44	116	18	25	114	102
49	155	35	83	97	35
35	95	56	48	130	39
58	25	35	82	325	35
Mean 85	82	70	70	129	42

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	79	83	86	87	88

Lights:	R	G	Y	B	W	P
Means:	42	70	70	82	85	129

*Least significant range at the 5% level.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.

portions of the spectrum.

In comparison of the mean values for apparent photosynthesis in these two experiments (Table 8, A and 9, A) it is well exemplified that with light intensity measurements in energy there are less differences among light qualities than when light intensity measurements are in ft-c. Thus, these results (Tables 8, A and 9, A) indicate that the action of 2,4-D is equally modified by all light qualities where the light intensity is adjusted at equal energy levels. On the other hand, where ft-c are used some light colors are more effective in promoting the action of 2,4-D on CO_2 uptake.

Low light intensity and 2% and 5% sucrose:500 ppm 2,4-D mixtures. Experiments were designed to test the effects of sucrose:2,4-D mixture solutions. The short-term light conditioning period was used with a light intensity of 600 $\mu w/cm^2$.

With the use of 2% sucrose:500 ppm 2,4-D mixture only red showed any significance in influencing the uptake and output of CO_2. Red was significant over warm white and green in interfering with CO_2 uptake at the 5% level (Table 10, A).

In promoting respiration, red was significant over warm white at the 5% level (Table 10, B). No other significance was observed among light qualities.

No significant differences were observed among light qualities in their effect on CO_2 uptake and output when the 5% sucrose:500 ppm 2,4-D mixture was used (Table 11). The

Table 10. Effects of short-term (5 days) light at 600 $\mu w/cm^2$ and 2% sucrose:500 ppm 2,4-D mixture on photosynthesis and respiration by mustard plants.

A. "Apparent Photosynthesis"- Differences in CO_2 uptake between control and treated plants (20 plants each) in microliters for one hour.

	W	B	G	Y	P	R
	95	114	67	86	324	120
	95	222	109	132	208	298
	74	204	28	206	83	185
	199	125	69	266	190	104
	162	102	255	120	238	426
	28	95	130	222	197	255
Mean	109	144	110	172	207	231

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	96	101	104	106	108

Lights:	W	G	B	Y	P	R
Means:	109	110	144	172	207	231

B. "Respiration"- Differences in CO_2 output between control and treated plants (20 plants each) in microliters for one hour.

	W	B	G	Y	P	R
	65	60	48	12	26	75
	69	62	74	101	51	173
	37	30	56	139	53	18
	51	76	81	33	122	104
	9	83	76	169	116	151
	34	61	28	88	109	72
Mean	44	62	60	90	80	99

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	45	48	49	50	51

Lights:	W	G	B	P	Y	R
Means:	44	60	62	80	90	99

*Least significant range at the 5% level.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.

Table 11. Effects of short-term (5 days) light at 600 $\mu w/cm^2$ and 5% sucrose:500 ppm 2,4-D mixture on photosynthesis and respiration by mustard plants.

A. "Apparent Photosynthesis"- Differences in CO_2 uptake between control and treated plants (20 plant each) in microliters for one hour.

	W	B	G	Y	P	R
	206	347	215	197	315	285
	157	44	201	243	130	407
	306	197	220	123	345	26
	146	46	123	37	27	373
	252	254	188	285	250	49
	190	405	111	213	171	222
Mean	210	216	176	183	207	227

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	136	142	147	150	152

Lights:	G	Y	P	W	B	R
Means:	176	183	207	210	216	227

B. "Respiration"- Differences in CO_2 output between control and treated plants (20 plants each) in microliters for one hour.

	W	B	G	Y	P	R
	108	382	65	167	460	295
	74	86	106	125	65	90
	212	83	109	95	77	212
	92	39	357	200	92	222
	196	184	97	155	30	106
	95	448	221	86	157	90
Mean	130	204	159	136	147	169

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	133	140	144	147	149

Lights:	W	Y	P	G	R	B
Means:	130	136	147	159	169	204

*Least significant range at the 5% level.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.

results indicated that 5% sucrose added to 2,4-D lessened the effects of 2,4-D sufficiently to eliminate any significance among light qualities.

Results of these experiments are, in general, in-agreement with the findings of Gentner and Hilton (30) who observed some reduced herbicidal effect of five phenylurea herbicides on barley plants with sucrose. Alvim (2) was able to control bean root dry weight reduction caused by GA with 10% sucrose sprays. Sucrose also lessened the injury from 2% urea spray.

Low light intensity and 5% sucrose:500 ppm 2,4-D vs. 500 ppm 2,4-D. This experimental test consisted of two chemical treatments and a light treatment. The light intensity was 600 $\mu w/cm^2$ using the short-term light conditioning period. Under each light quality one half of the plants (6 containers) were treated with a mixture of a solution of 5% sucrose:500 ppm 2,4-D, while a second half (6 containers) were treated with a 500 ppm 2,4-D solution alone. CO_2 exchange measurements were made, and the differences in microliters of CO_2 between the two treatments determined for each light quality used. The results are presented in Table 12. Among light qualities there were no significant differences at the 5% level for either CO_2 uptake or output. Yet, it may be noted that in a former test there were significances among light qualities in promoting 500 ppm 2,4-D interference in CO_2 uptake (Table 6, A). Therefore, the 5% sucrose:500 ppm 2,4-D mixture eliminated any significance among light qualities in

Table 12. Effects of short-term (5 days) light at 600 $\mu w/cm^2$ 5% sucrose:500 ppm 2,4-D mixture and 500 ppm 2,4-D on photosynthesis and respiration by mustard plants.

A. "Apparent Photosynthesis"- Differences in CO_2 uptake between the mixture treated and 2,4-D treated plants (20 plants each) in microliters for one hour.

W	B	G	Y	P	R
21	532	35	46	342	35
49	106	44	111	30	232
44	65	16	49	44	37
7	12	90	136	229	194
132	241	49	264	39	18
16	37	39	266	150	26
Mean 45	166	46	145	139	90

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	137	144	148	151	154

Lights:	W	G	R	P	Y	B
Means:	45	46	90	139	145	166

B. "Respiration"- Differences in CO_2 output between the mixture treated and 2,4-D treated plants (20 plants each) in microliters for one hour.

W	B	G	Y	P	R
32	140	102	67	189	60
28	143	100	113	116	90
28	51	65	14	74	247
42	5	86	39	248	185
183	100	0	229	67	70
32	44	46	486	139	58
Mean 58	80	66	158	139	118

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	118	124	128	130	132

Lights:	W	G	B	R	P	Y
Means:	58	66	80	118	139	158

*Least significant range at the 5% level.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.

inhibiting CO_2 uptake (Table 11, A). These results show that with 500 ppm of 2,4-D the 5% sucrose lessens the interference in CO_2 uptake. Thus in some manner the sucrose has decreased the effectiveness of the herbicide in disrupting the metabolic reactions involved in CO_2 uptake.

High light intensity and 1000 ppm 2,4-D. An experiment was designed to study the effects of high light intensity. The highest light intensity obtainable was used. This intensity was measure in ft-c and the long-term light conditioning period used. The lamps used were the only type available for obtaining high intensity at the time this experiment was conducted. The intensities for blue (VB), and red (VR) were highest while the intensity for pink was lowest. CO_2 exchange measurements were made on control and 1000 ppm 2,4-D treated plants. The differences in CO_2 uptake and output between control and treated plants in microliters are shown in Table 13.

Among light qualities pink was most effective in promoting 2,4-D interference with CO_2 uptake. Pink was significant above all lights except yellow at the 5% level. Yellow was significant over warm white. No significant differences were observed among blue, red, green, and yellow lights. Although blue and red light had the highest light intensities, they were only slightly more effective than warm white in causing 2,4-D to inhibit CO_2 uptake (Table 13, A).

The stimulatory effect of 2,4-D on CO_2 output was significantly influenced only by red light. Red was significant

Table 13. Effects of long-term (20 days) light at high intensities and 1000 ppm 2,4-D on photosynthesis and respiration by mustard plants.

A. "Apparent Photosynthesis"- Differences in CO_2 uptake between control and treated plants (20 plants each) in microliters for one hour.

W (954)[a]	VB (1710)	G (954)	Y (954)	P (465)	VR (1480)
210	196	67	168	90	146
449	539	446	403	529	391
141	111	352	289	590	65
262	245	272	570	443	423
128	173	180	453	417	213
30	77	313	275	525	162
Mean 203	224	272	360	432	233

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	136	143	148	151	158

Lights:	W	VB	VR	G	Y	P
Means:	203	224	233	272	360	432

B. "Respiration"- Differences in CO_2 output between control and treated plants (20 plants each) in microliters for one hour.

W (954)[a]	VB (1710)	G (954)	Y (954)	P (465)	VR (1480)
99	162	37	138	90	412
178	261	222	150	211	88
48	62	92	150	116	194
148	222	60	225	180	490
24	104	304	248	278	102
53	363	53	139	187	287
Mean 92	196	128	175	177	262

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	123	129	134	136	138

Lights:	W	G	Y	P	VB	VR
Means:	92	128	175	177	196	262

*Least significant range at the 5% level.
[a]Parentheses enclose ft-c intensities.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.

over warm white at the 5% level (Table 13, B). No significance was observed in any other comparison among light qualities.

Several workers (53, 57, 61) using different plants have reported increased CO_2 uptake and output with rather high light intensity. In fact, intensities ranged from 0 to 6000 ft-c. For this reason more significant differences among light qualities with high light intensity were expected in causing 2,4-D inhibition of CO_2 uptake and output than observed in the data presented (Table 13). No reasonable explanation is offered for the absence of more significant differences among light qualities. It is possible that species differences are responsible for the lack of more significant differences.

Long-term light conditioning vs. short-term light conditioning at 1000 ft-c and 1000 ppm 2,4-D. This test was concerned with an evaluation of the effects of yellow and green lights as compared to warm white on CO_2 exchange of 2,4-D treated and control plants. The experiment was designed to incorporate both long-term and short-term light conditioning periods. The corrected light intensity for all light qualities was 1000 ft-c. A 1000 ppm 2,4-D solution was used. Table 14 shows the results of the CO_2 exchange measurements as differences in CO_2 uptake and output between control and 2,4-D treated plants.

No significant differences in CO_2 uptake were observed for the different spectral regions either with the long-term light conditioning period or the short-term light conditioning

Table 14. Effects of long-term (20 days) and short-term (5 days) light at 1000 ft-c and 1000 ppm 2,4-D on photosynthesis and respiration by mustard plants.

A. "Apparent Photosynthesis"- Differences in CO_2 uptake between control and treated plants (20 plants each) in microliters for one hour.

W^1	Y^1	G^1	W^2	Y^2	G^2
364	213	384	98	398	312
79	123	164	303	92	155
396	35	199	245	95	374
287	303	114	220	167	81
386	114	252	294	229	160
38	197	181	195	46	169
Mean 258	164	216	226	171	208

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	127	134	138	141	143

Lights:	Y^1	Y^2	G^2	G^1	W^2	W^1
Means:	164	171	208	216	226	258

B. "Respiration"- Differences in CO_2 output between control and treated plants (20 plants each) in microliters for one hour.

W^1	Y^1	G^1	W^2	Y^2	G^2
266	88	153	234	172	188
69	95	46	243	115	96
72	58	123	9	30	202
76	60	30	174	142	176
97	75	67	227	179	130
104	76	39	18	67	95
Mean 114	75	76	151	118	148

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	67	71	73	75	76

Lights:	Y^1	G^1	W^1	Y^2	G^2	W^2
Means:	75	76	114	118	148	151

*Least significant range at the 5% level.
[1]Long-term light.
[2]Short-term light.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.

period. Also, no significant differences were observed for the same light quality with either light conditioning period. In fact, the difference between the means for the same light quality for both light conditioning periods was small for each of the light qualities used (see Means in Table 14, B).

CO_2 output was enhanced more by 2,4-D with the short-term light conditioning period than with the long-term light conditioning. Only warm white of the short-term was slightly significant over yellow of the long-term light conditioning.

Generally, yellow and green light are accepted to be poor for plant growth. Berrie (9) in a study relating the effect of sucrose sprays on the growth of tomato plants found poor growth under green light as compared to daylight and yellow light. A suppressive nature of green light has been emphasized by Klein (44).

Effects of Light Quality and 2,4-D on Dry Weight

Since dry weight increment is due to the excess of photosynthesis over respiration, any conditions favorable for high photosynthetic efficiency should result in an increase in dry weight. Since many investigators have concluded that light qualities may influence the effect of 2,4-D on photosynthesis, several studies were conducted to determine how some favorable photosynthetic conditions would modify the action of 2,4-D on dry weight yield. Also, comparisons were made of dry weight yield among light qualities where the

light intensity was measured in microwatts per square centimeter.

High light intensity and 1000 ppm 2,4-D. Six different kinds of fluorescent lamps were used. Two were General Electric T-8 slimline fluorescent lamps (R and W, see Table 1 and Fig. 1) and four were Sylvania Electric VHO fluorescent lamps (VR, VB, VW, and VCW, see Table 1 and Fig. 2). The long-term light conditioning period was employed in this test. The light intensity was 1500 ft-c for all qualities except General Electric red (R), which was 454 ft-c since this was the maximum obtainable with this quality. At the conclusion of the light conditioning period, twelve replicates, two from each of the six rotating tables, were treated with the solution of 2,4-D whlie twelve replicates were retained as controls (untreated) for each light quality. The containers of plants were returned to their original positions under the lights after the spray solution dried on the foliage. A post-spray period of ten days was given all plants (control and treated). Plant tops were harvested at the end of the post-spray period and the dry weights taken after drying for ten days. The percentage reduction in dry weight by 2,4-D was determined. Results are shown in Table 15.

Blue light was statistically less effective in promoting the 2,4-D effect on mustard than the other five light qualities at the 5% level. Both red light qualities were significantly more effective than blue at the 1% level in causing dry weight reduction by 2,4-D. No significant differences existed at the 1% level between any of the other

Table 15. Effects of long-term (20 days) light at high intensity and 1000 ppm 2,4-D on dry weight of mustard plants.

Percentage reduction in dry weight of 2,4-D treated plants (20 plants each) below that of control plants (20 plants each).

VR (1500)[a]	R (454)	VB (1500)	VW (1500)	W (1500)	VCW (1500)
19.1	50.5	29.1	26.6	6.3	45.7
46.2	38.8	30.0	37.5	35.6	33.0
44.8	53.0	38.9	27.2	40.8	42.1
44.7	53.7	26.1	36.0	45.6	43.7
18.4	28.3	8.4	45.5	47.6	43.6
47.2	52.6	21.8	35.9	43.2	48.1
51.7	33.6	36.7	42.7	40.1	43.1
54.5	48.0	30.8	39.1	45.2	8.3
8.7	33.7	37.1	43.9	53.1	43.9
40.1	42.7	13.1	41.7	40.0	49.7
59.6	54.1	33.6	28.5	35.1	43.8
68.0	58.9	14.6	44.5	43.0	39.2
Mean 41.9	45.6	26.7	37.4	39.6	40.4

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	9.7	10.2	10.5	10.8	10.9

Lights:	VB	VW	W	VCW	VR	R
Means:	26.7	37.4	39.6	40.4	41.9	45.6

*Least significant range at the 5% level.

[a]Parentheses enclose ft-c intensities.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.

light qualities. The choice of lamps for this experiment was based on the fact that generally 2,4-D was most effective in the presence of red and blue light with somewhat low light intensities. Because the maximum obtainable light intensity for General Electric red (R) was very low, this permitted a vey substantial comparison with higher light inintensity. The greatest reduction in dry weight yield was obtained with the low intensity red light. These results indicate that low light intensities are most effective in influemcing the action of 2,4-D.

Low light intensity, 1000 ppm 2,4-D, and 5% sucrose. An experiment was conducted to measure the effects of light quality in relation to its modification of the 2,4-D action with and without sucrose. There were four treatments: (i) control; (ii) 5% sucrose; (iii) 1000 ppm 2,4-D; and (iv) 5% sucrose:1000 ppm 2,4-D mixture. In evaluating the light qualities the light intensity was 600 $\mu w/cm^2$ for all light colors and the short-term light conditioning period was used. A post-spray period of ten days was given all plants resulting in a total of fifteen days illumination.

Control (Table 16, A). All plants grew very well under lights of all qualities. The greatest increase in dry weight occurred in plants illuminated with red light. Red was significant over blue, green, yellow, and warm white, while pink was significant only over blue at the 5% level. Blue was least effective in causing dry weight increase, followed by green, yellow, and warm white although differences between these lights were not significantly different (Table

Table 16. Effects of short-term (5 days) light at 600 μw/cm2 of six different light qualities, and 5% sucrose, 1000 ppm 2,4-D, and 5% sucrose:1000 ppm 2,4-D mixture on dry weight (mgms) production of mustard plants.

A. Control:

W	B	G	Y	P	R
629	239	624	529	529	974
494	644	574	604	864	984
684	384	404	599	869	1049
544	479	379	489	434	854
639	539	409	539	694	574
529	494	719	404	749	579
Mean 586	463	518	527	690	836

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	170	179	184	188	191

Lights:	B	G	Y	W	P	R
Means:	463	518	527	586	690	836

B. Sucrose Treated:

W	B	G	Y	P	R
369	589	409	604	769	909
539	544	544	489	269	929
559	564	279	639	769	569
664	539	459	489	414	759
569	339	514	554	479	989
674	544	619	594	909	749
Mean 562	520	471	562	602	817

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	176	185	191	195	198

Lights:	G	B	Y	W	P	R
Means:	471	520	562	562	602	817

Table 16. -Continued

C. 2,4-D Treated:

W	B	G	Y	P	R
284	209	199	324	374	299
24	114	174	109	184	289
224	264	99	214	244	184
199	119	184	284	164	169
214	159	234	314	344	339
284	324	264	274	414	379
Mean 205	198	192	253	287	276

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	71	75	77	78	80

Lights:	G	B	W	Y	R	P
Means:	192	198	205	253	276	287

D. Sucrose:2,4-D Mixture Treated:

W	B	G	Y	P	R
309	329	164	179	444	289
199	159	339	339	344	494
139	244	169	264	134	354
119	164	229	204	169	269
139	214	189	279	359	424
274	274	194	254	379	374
Mean 196	231	214	253	305	367

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	88	93	96	98	99

Lights:	W	G	B	Y	P	R
Means:	196	214	231	253	305	367

*Least significant range at the 5% level.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.

16, A). At the 1% level red showed a similar significance over all lights except pink.

Sucrose (Table 16, B). The dry weight production of plants treated with sucrose was greatest in those plants irradiated with red light. At the 5% level red was significant over green, blue, yellow, warm white, and pink. No significance existed among green, blue, yellow, warm white, and pink (Table 16, B). Only plants illuminated with blue, and yellow gained in dry weight as a result of the exogenous sucrose supply. Berrie (9) found that tomato plants irradiated with yellow light made better use of applied sugars than did those irradiated with daylight and green light under a 16 hour daylength.

2,4-D (Table 16, C). Pink light was most efficient in causing dry weight increase in 2,4-D treated plants. Next was red, followed by yellow, warm white, blue, anf green. At the 5% level pink was significant over green, blue, and warm white. Red was found to be significant over green and blue. No significant differences in dry weight yield was noted among green, blue, warm white, and yellow. The differences between warm white, yellow, and red were non-significant. Also differences found between red and pink were non-significant (Table 16, C).

Sucrose:2,4-D mixture (Table 16, D). Plants treated with a sucrose:2,4-D mixture produced the greatest dry weight under red, followed by pink, yellow, blue, green, and warm white. Red was significant over all lights except pink at the 5% level. Warm white was significantly less effective

than pink. There were no significant differences between warm white, green, blue, and yellow nor were there any significant differences between green, blue, yellow, and pink Table 16, D). At the 1% level red was significant over warm white, green, and blue.

Control vs. sucrose (Table 17, A). The differences in dry weight production between control and sucrose treated plants were not significant among light qualities (Table 17, A). The sucrose sprayed plants irradiated with blue and yellow produced more dry weight than control plants under the same lights (Table 16, A and B).

Control vs. 2,4-D (Table 17, B). 2,4-D significantly reduced the dry weight yield of plants illuminated with red light. At the 5% level red was significantly more effective in promoting the 2,4-D effect on dry weight increase over blue, yellow, and green. The differences among means for warm white, pink, and red were statistically non-significant as were the differences among means for blue, yellow, green, warm white, and pink (Table 17, B). At the 1% level red was significant over blue and yellow.

Control vs. sucrose:2,4-D mixture (Table 17, C). There was considerable reduction in dry weight by the sucrose: 2,4-D mixture treatment. However, differences among light qualities were statistically non-significant. The greatest reduction was found with red light, followed by warm white, pink, green, yellow, and blue (Table 17, C).

These results (Table 17, B and C) indicated that

Table 17. Comparisons between treatments presented in Table 16.

A. Control vs. Sucrose Treated (Differences in dry weight between control and sucrose treated):

W	B	G	Y	P	R
260	350	215	75	240	65
45	100	30	115	595	55
125	180	125	40	100	480
120	60	80	0	20	95
70	200	105	15	215	415
145	50	100	190	160	170
Mean 128	157	109	72	222	213

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	158	166	171	174	177

Lights:	Y	G	W	B	R	P
Means:	72	109	128	157	213	222

B. Control vs. 2,4-D Treated (Reduction in dry weight by 2,4-D below that of control plants):

W	B	G	Y	P	R
345	30	425	205	155	675
470	530	400	495	680	695
460	120	305	385	625	865
345	360	195	205	270	685
425	380	175	225	350	235
245	170	455	130	335	200
Mean 382	265	326	274	402	559

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	184	193	200	203	206

Lights:	B	Y	G	W	P	R
Means:	265	274	326	382	402	559

Table 17. -Continued

C. Control vs. Sucrose:2,4-D Mixture Treated (Reduction in dry weight by mixture below that of control plants):

	W	B	G	Y	P	R
	320	90	460	350	85	685
	295	485	235	265	520	490
	545	140	235	335	735	695
	425	315	150	285	265	585
	500	325	220	260	335	150
	255	220	525	150	370	205
Mean	390	262	304	274	385	468

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	204	214	221	226	229

Lights:	B	Y	G	P	W	R
Means:	262	274	304	385	390	468

D. Sucrose Treated vs. 2,4-D Treated (Reduction in dry weight by 2,4-D below that of sucrose treated plants):

	W	B	G	Y	P	R
	85	380	210	280	395	610
	515	430	370	380	85	640
	335	300	180	425	525	385
	465	420	275	205	250	590
	355	180	280	240	135	650
	390	220	355	320	495	370
Mean	358	322	278	308	314	541

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	160	168	174	177	180

Lights:	G	Y	P	B	W	R
Means:	278	308	314	321	358	541

Table 17. -Continued

E. Sucrose Treated vs. Sucrose:2,4-D Mixture Treated (Reduction in dry weight by mixture below that of sucrose treated plants):

W	B	G	Y	P	R
60	260	245	425	325	620
340	385	205	150	75	435
420	320	110	375	635	215
545	375	230	285	245	490
430	125	325	275	120	565
400	270	425	340	530	375
Mean 366	289	257	308	322	450

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	181	190	196	200	203

Lights:	G	B	Y	P	W	R
Means:	257	289	308	322	366	450

F. Sucrose:2,4-D Mixture Treated vs. 2,4-D Treated (Differences in dry weight between mixture treated and 2,4-D treated plants):

W	B	G	Y	P	R
25	120	35	145	70	10
175	45	165	230	160	205
85	20	70	50	110	170
80	45	45	80	5	100
75	55	45	35	15	85
10	50	70	20	35	5
Mean 75	56	72	93	66	96

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	55	58	60	61	62

Lights:	B	P	G	W	Y	R
Means:	55	65	71	75	93	95

*Least significant range at the 5% level.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.

yellow and green lights are equally effective as blue in promoting the 2,4-D effect on dry weight reduction where light intensity is measured as incident energy. This was true with 2,4-D alone and with the sucrose:2,4-D mixture (Table 17, B and C).

Sucrose vs. 2,4-D (Table 17, D). Red light was significant over green, yellow, pink, blue, and warm white in reducing dry weight of 2,4-D treated plants below that of sucrose treated plants at the 5% level. No significant reduction occurred among these latter five lights (Table 17, D). At the 1% level red was significant over green in promoting the 2,4-D effect.

Sucrose vs. sucrose:2,4-D mixture (Table 17, E). The differences among light qualities in causing a reduction in dry weight yield by the sucrose:2,4-D mixture below that of the sucrose treated plants were non-significant at the 5% level. Although non-significant, the greatest reduction was obtained with red light, followed by warm white, pink, yellow, blue, and green (Table 17, E). It is evident from these results that the addition of sucrose reduced the effect of 2,4-D under red light in the reduction of dry weight yield of 2,4-D treated plants below that of sucrose treated plants (see Table 17, D).

Sucrose:2,4-D mixture vs. 2,4-D (Table 17, F). Differences among light qualities of the differences in dry weight yield between the sucrose:2,4-D mixture treated and 2,4-D treated plants were non-significant (Table 17, F).

Although the sucrose:2,4-D mixture was not significantly less in its effect on dry weight production than 2,4-D alone there was a general reduction in the 2,4-D effect by the addition of sucrose under all lights (Table 16, C and D).

Low light intensity, 1000 ppm 2,4-D, and 10% sucrose. Since 5% sucrose lessens the 2,4-D effect under various light qualities a similar experiment was conducted using a higher sucrose concentration (10%). With the exception of an increase in the sucrose concentration all other conditions were precisely the same as those for the test conducted with 5% sucrose.

Control (Table 18, A). Dry weight in mustard was greatest under red light, followed by pink, yellow, green, warm white, and blue. Statistically, red was significant over all light qualities in promoting dry weight yield at the 5% level. The differences in yield obtained under pink and yellow were significant over blue at the 5% level. There were no other significant differences among light qualities (Table 18, A). At the 1% level dry weight production was significantly greater under red than under blue, warm white, green, and yellow. Pink was more efficient than blue in enhancing dry weight production at the 1% level.

Sucrose (Table 18, B). The results (Table 18, B) showed that red light was more efficient in promoting dry weight production of sucrose treated plants. The order of efficiency for light qualities on dry weight yield of sucrose treated plants was the same as with control plants (Table 18, A). The decreasing order of efficiency was: red, pink, yellow,

Table 18. Effects of short-term (5 days) light at 600 μw/cm^2 of six different light qualities, and 10% sucrose, 1000 ppm 2,4-D, and 10% sucrose:1000 ppm 2,4-D mixture on dry weight (mgms) production of of mustard plants.

A. Control:

W	B	G	Y	P	R
747	867	794	864	704	1017
1177	802	1104	1349	1199	1502
1162	1217	1079	1354	1509	1847
1422	1117	1414	1499	1709	1637
1202	1047	1289	1269	1179	1322
707	667	934	819	1219	1372
Mean 1070	953	1102	1192	1253	1450

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	173	182	188	191	194

Lights:	B	W	G	Y	P	R
Means:	953	1070	1102	1192	1253	1450

B. Sucrose Treated:

W	B	G	Y	P	R
992	727	1044	929	1184	1467
1292	787	1184	1454	1594	1697
1512	1337	1234	1509	1374	1712
1192	1017	1259	1364	1489	1872
1052	1037	1449	1304	1929	1642
737	827	1094	1039	1089	1352
Mean 1130	955	1211	1266	1443	1624

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	185	194	200	204	207

Lights:	B	W	G	Y	P	R
Means:	955	1130	1211	1266	1443	1624

Table 18. -Continued

C. 2,4-D Treated:

W	B	G	Y	P	R
297	437	419	359	429	522
507	412	534	504	589	742
592	532	649	594	604	587
442	302	594	644	664	662
467	412	614	614	419	727
442	337	514	524	459	562
Mean 458	405	554	540	527	634

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	86	91	94	96	97

Lights:	B	W	P	Y	G	R
Means:	405	458	527	540	554	634

D. Sucrose:2,4-D Mixture Treated:

W	B	G	Y	P	R
612	402	539	434	499	522
552	422	609	734	699	647
537	597	754	589	789	662
692	602	529	739	974	747
662	442	784	684	709	727
492	442	684	579	469	682
Mean 591	484	650	626	690	664

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	112	118	122	124	126

Lights:	B	W	Y	G	R	P
Means:	484	591	626	650	664	690

*Least significant range at the 5% level.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.

green, warm white, and blue. The plants illuminated with red yielded significantly greater dry weight than those illuminated with blue, warm white, green, and yellow. Pink exhibited significance over blue, warm white, and green in the production of dry weight. Both yellow and green were found to be significantly more efficient in causing dry weight increase than blue at the 5% level (Table 18, B).

2,4-D (Table 18, C). In this test also, the red light produced the greatest dry weight. The next greatest yield was obtained with green, followed by yellow, pink, warm white, and blue. The mean dry weight yield produced under red light was significantly higher than that of blue, warm white, pink, and yellow. Green was significantly more effective than blue and warm white. Yellow and pink showed significance over blue (Table 18, C).

Sucrose:2,4-D mixture (Table 18, D). When the mean dry weight yields (Table 18, D) of the sucrose:2,4-D mixture treated plants were compared among light qualities the greatest dry weight increase was found under pink light. Following pink in order of effectiveness were: red, green, yellow, warm white, and blue. Blue was significantly less effective in promoting dry weight increase than all lights except warm white at the 5% level.

Control vs. sucrose (Table 19, A). The 10% sucrose treatment was found to be more effective in causing dry weight increase than 5% sucrose under all lights except blue (Tables 17, E and 19, E). The mean dry weight of sucrose treated plants was greater than that for control plants under all

Table 19. Comparisons between treatments presented in Table 18.

A. Control vs. Sucrose Treated (Differences in dry weight between control and sucrose treated):

W	B	G	Y	P	R
245	140	250	65	480	450
115	15	80	105	395	195
350	120	155	155	135	135
230	100	155	135	220	235
150	10	160	35	750	320
30	160	160	220	130	20
Mean 187	91	160	119	352	226

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	155	163	168	172	174

Lights:	B	Y	G	W	R	P
Means:	91	119	160	187	226	352

B. Control vs. 2,4-D Treated (Reduction in dry weight by 2,4-D below that of control plants):

W	B	G	Y	P	R
450	430	375	505	275	495
670	390	570	845	610	760
570	685	430	760	905	1260
980	815	820	855	1045	975
735	635	675	655	760	595
265	330	420	295	760	810
Mean 612	548	548	652	726	816

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	186	195	202	205	209

Lights:	B	G	W	Y	P	R
Means:	548	548	612	652	726	816

Table 19. -Continued

C. Control vs. Sucrose:2,4-D Mixture Treated (Reduction in dry weight by mixture below that of control plants):

W	B	G	Y	P	R
135	467	255	430	205	495
625	380	495	615	500	855
625	620	325	765	720	1185
730	515	885	760	735	890
540	605	505	585	470	595
215	225	250	240	750	690
Mean 478	469	452	566	563	785

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	184	194	200	204	207

Lights:	G	B	W	P	Y	R
Means:	452	469	478	563	566	785

D. Sucrose Treated vs. 2,4-D Treated (Reduction in dry weight by 2,4-D below that of sucrose treated plants):

W	B	G	Y	P	R
695	290	625	570	755	945
785	375	650	950	1005	955
920	805	585	915	770	1125
750	715	665	720	825	1210
585	625	835	690	1510	915
295	490	580	515	630	790
Mean 672	550	657	727	916	990

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	208	219	226	231	234

Lights:	B	G	W	Y	P	R
Means:	550	657	672	727	916	990

Table 19. -Continued

E. Sucrose Treated vs. Sucrose:2,4-D Mixture Treated (Reduction in dry weight by mixture below that of sucrose treated plants):

W	B	G	Y	P	R
380	325	505	495	685	945
740	365	575	720	895	1050
975	740	480	920	585	1050
500	415	730	625	515	1125
390	595	665	620	1220	915
245	385	410	460	620	670
Mean 538	471	561	640	753	959

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	203	213	220	224	228

Lights:	B	W	G	Y	P	R
Means:	471	538	561	640	753	959

F. Sucrose:2,4-D Mixture Treated vs. 2,4-D Treated (Differences in dry weight between mixture treated and 2,4-D treated plants):

W	B	G	Y	P	R
315	35	120	75	70	0
45	10	75	230	110	95
55	65	105	5	185	75
250	300	65	95	310	85
195	30	170	70	290	0
50	5	170	55	10	120
Mean 152	74	118	88	162	62

p:	(2)	(3)	(4)	(5)	(6)
LSR*:	108	113	117	119	121

Lights:	R	B	Y	G	W	P
Means:	62	74	88	118	152	162

*Least significant range at the 5% level.

Note: Any two means not underscored by the same line are significantly different, whereas any two means underscored by the same line are not significantly different.

light qualities (Table 18, A and B). Plants illuminated with pink most effectively utilized sucrose. Pink was followed by red, warm white, green, yellow, and blue in mean dry weight increase of sucrose treated plants above that of control plants. At the 5% level pink was significant over blue, yellow, green, and warm white. Red was significant only over blue (Table 19, A).

Control vs. 2,4-D (Table 19, B). Among light qualities red was more effective in promoting 2,4-D interference with dry weight increase. The next most effective lights were in the following order: pink, yellow, warm white, green, and blue. At the 5% level only red was significant over blue, green, and warm white (Table 19, B).

Control vs. sucrose:2,4-D mixture (Table 19, C). Table 19, C shows the reduction in dry weight by the sucrose: 2,4-D mixture below that of controls. The greatest reduction was found in plants illuminated with red light. The next greatest reductions in dry weight were obtained in the following order: yellow, pink, warm white, blue, and green. Red was significant over all lights in promoting the reductive effect on dry weight by the sucrose:2,4-D mixture below that of controls. At the 1% level only green, blue, and warm white were less effective than red.

Sucrose vs. 2,4-D (Table 19, D). The reduction of dry weight by 2,4-D below sucrose treated plants was markedly influenced by light quality. The greatest difference in dry weight yield between sucrose treated and 2,4-D treated

plants occurred in plants irradiated with red and pink. Following these in order of effectiveness were: yellow, warm white, green, and blue. Red was shown to be significantly more effective than blue, green, warm white, and yellow. Pink was significant over blue, green, and warm white at the 5% level (Table 19, D). At the 1% level red was significant over blue, green, and warm white, while pink was significant only over blue.

Sucrose vs. sucrose:2,4-D mixture (Table 19, E). The presence of sucrose lessened the reductive effect of 2,4-D under all light qualities. Although dry weight reduction was decreased, red light remained most effective in promoting the effect of 2,4-D, followed by pink, yellow, green, warm white, and blue. Red was significantly more influential in promoting 2,4-D interference in dry weight production than all lights at the 5% level. Pink was significantly more influential than blue (Table 19, E).

Sucrose:2,4-D mixture vs. 2,4-D (Table 19, F). Differences among light qualities for differences in dry weight yield between sucrose:2,4-D mixture treated plants and 2,4-D treated plants were non-significant. The greatest difference was found with pink illumination. The next greatest was found with warm white, followed by green, yellow, blue, and red (Table 19, A).

CONCLUSIONS

The modifying effect of light quality of 2,4-D action with mustard plants has been shown to be variable. Here, the "2,4-D action" or "2,4-D effect" refers to the inhibition of photosynthesis, stimulation of respiration, and reduction in dry weight of mustard plants by 2,4-D. In most of the experiments conducted, where light intensity was measured as ft-c, generally red, and blue light were most effective in promoting the action of 2,4-D. On the other hand, yellow, and green were generally least effective. However, with light intensity measured as incident energy the influence of light quality on the 2,4-D action varies greatly with different colors. For example green light is often more effective than blue. Since illuminance measurements (ft-c) are based on the sensitivity curve of the human eye which has its maximum in the green, equal intensities in ft-c for light qualities would definitely give different energy levels for light qualities being compared. No evidence has been offered that plants respond to light the same as the human eye, but it is generally accepted that plants respond to all portions of the visible spectrum. Thus it is evident from the results of these experiments that light intensity should be measured in energy and not illuminance for the better evaluation of light quality effects.

It may be concluded that the action of 100 ppm 2,4-D on CO_2 uptake and output was not significantly influenced by light quality at low light intensity. This non-significant

effect of light quality was found with both short and long-term light conditioning.

Results from experiments with low light intensity and 500 ppm 2,4-D showed that pink light was most effective in promoting 2,4-D interference in CO_2 uptake, next was red, followed by yellow, green, blue, and warm white. Here the light intensity was measured as incident energy using the short-term light conditioning period. However, with long-term light conditioning and light intensity measured in ft-c warm white light was most effective, followed by blue, green, red, pink, and yellow. Respiration was stimulated by 500 ppm 2,4-D under all light qualities, but significantly so only under red light.

Light quality was very effective in modifying the action of 2,4-D at 1000 ppm, with low intensity light measured in ft-c, and when short-term light conditioning was used. Blue light was most effective in promoting 2,4-D interference in CO_2 uptake. Following blue in order of effectiveness were: pink, red, warm white, yellow, and green. CO_2 output was enhanced by 2,4-D under all lights, but differences between light qualities were non-significant. On the other hand, where low light intensity was measured as incident energy with short-term light conditioning, light quality was less effective in promoting 2,4-D interference with CO_2 uptake. However, CO_2 output was significantly enhanced by 2,4-D under red, and warm white light.

The fact that lower concentrations of herbicides

have less effect on CO_2 uptake and output than higher concentrations was pointed out by other workers (5, 45, 79). A similar conclusion is reached here based on the fact that the degree of effectiveness of 2,4-D under different light qualities increased with an increase in concentration of 2,4-D.

The presence of 2% sucrose mixed with 500 ppm 2,4-D lessened the effect of 2,4-D interference in CO_2 uptake and output by mustard plants under all light qualities. Only red light promoted a significant 2,4-D interference in CO_2 uptake and output. With a higher sucrose concentration (5%) the significant modifying effects among light qualities on the 2,4-D action were eliminated. Thus the 2,4-D effect on mustard plants observed under different light qualities may be decreased with the addition of sucrose. It may be that the effect of 2,4-D on photosynthesis reduces the production of carbohydrates by inhibiting CO_2 uptake which could possibly be associated with the opening and closing of the stomates. The addition of sucrose supplies carbohydrates which the plants assimilate, thereby the effect of 2,4-D is overcome. However, stimulation of respiration by 2,4-D would result in considerable depletion of the added carbohydrate. Although 5% sucrose eliminated significant differences among light qualities in modifying the 2,4-D action, the reduced effect was not significant over the 2,4-D effect without sucrose added. A similar reduction of an inhibitory effect of several urea herbicides at low concentration on leaf development by

sucrose was reported by Gentner and Hilton (30).

The influence of light quality on the 2,4-D action was not greatly enhanced with high light intensity and long-term light conditioning. In fact, 2,4-D inhibition of CO_2 uptake was least with light qualities having the highest intensities except for warm white. The order of decreasing effectiveness in promoting the action of 2,4-D was: pink, yellow, green, red, blue, and warm white. However, the greatest 2,4-D stimulation of CO_2 output was found in plants under light qualities with the highest intensities. This conclusion is partly in agreement with the findings of Jordan, Dunham, and Linck (41) in that they observed the greatest response of flax to 2,4-D with low intensity and least with high intensity.

Among light qualities with high intensity, dry weight reduction by 2,4-D was greatest with red (VR), and least with blue (VB). This agrees with the report of Tregunna, Krotkov, and Nelson (70) that leaves illuminated with red light generally absorbs larger amounts of CO_2 than leaves illuminated with blue. Thus the greatest reduction in dry weight by 2,4-D under red light indicate a greater interference in CO_2 uptake with red irradiation than with blue irradiation of mustard plants treated with 2,4-D. The greatest dry weight reduction occurred in plants illuminated with low intensity red light (R). Again, light of low intensity was more effective in promoting the 2,4-D effect on plant growth.

Red, and pink light with some exceptions were most effective in promoting dry weight increase over other light

colors in experiments with low intensity measured as incident energy. This was for 2,4-D treated plants with and without 5% and 10% sucrose, and short-term light conditioning. The 2,4-D effect was lessened by 10% sucrose under all light qualities.

The fact that considerable external morphological differences usually appear with long-term light conditioning may be an important factor when large differences in CO_2 uptake and output are found among light qualities. It is very likely that with an increased leaf area more stomates are present which would have a direct relation to the CO_2 exchange. Also, the possibility of more cells per unit leaf area would have some bearing on the photosynthetic and respiratory activities. Future studies of the effect of light quality on plant morphology should yield interesting results.

In all future experiments dealing with the measurement of photosynthesis (CO_2 uptake) and respiration (CO_2 output) attempts should be made to decrease variability between replications.

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